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Estimation of Direct and Maternal Additive and Heterotic Genetic Effects for Preweaning Traits in Beef Cattle.

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ESTIMATION OF DIRECT AND MATERNAL ADDITIVE AND HETEROTIC GENETIC EFFECTS FOR PREWEANING TRAITS IN BEEF CATTLE

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Abstract

Progeny records from 4 generations of a rotational crossbreeding experiment were fitted to a regression equation to obtain estimates of direct and maternal additive (Ig, Mg) and heterotic (Ih, Mh) genetic effects of preweaning traits for Angus (A), Brahman (B), Charolais (C), Hereford (H) breeds and their combinations. These estimates were fitted to prediction equations to compare preweaning performance of breed groups under different mating systems. Heterosis estimates were used to compute expected heterosis for each rotational cross. The C had the largest Ig estimate for BWT (5.2 kg), ADG (.074 kg/d) and WWT (22.1 kg) while H had the largest Ig estimate for SCORE (.73 units). Angus and C had similar and larger Mg estimates for BWT than H and B. Angus and B had the lowest Ig and Mg estimates, respectively, of -4.2 kg for BWT. The B had the largest Mg estimate (.070 kg/d) for ADG. Brahman and C had similar and larger Mg estimates for WWT and SCORE than A and H. The H had the lowest Mg estimate for ADG (-.107 kg/d), WWT (-23.0 kg) and SCORE (-.95 units). Brahman crosses (AB, BC and BH) had the largest Ih estimates for all preweaning traits. Brahman crosses also had the lowest Mh estimates for BWT. Except for BH cross, Brahman crosses had the lowest Mh estimates for ADG, WWT and SCORE. Hereford crosses (AH, BH and CH) had the largest Mh estimates for ADG, WWT and SCORE.

Brahman- and Charolais-sired crossbred calves generally had larger predicted BWT, ADG and WWT than those sired by A and H bulls. Brahman-Charolais and CB F1 cross calves had the largest predicted ADG and WWT. Angus- and Hereford-sired backcross calves generally had larger predicted SCORE than backcross calves sired by B and C bulls. Most stabilized rotational crossbred calves with more B and C breeding had the largest predicted ADG and WWT while those with more A and H breeding had the largest predicted SCORE. Comparisons of predicted vs realized heterosis suggested the presence of unaccounted variation in the expression of heterosis. The sign of the differences suggested that recombination loss effects may be positive or negative. Comparisons of breed group and genetic effects models suggested no evidence of epistasis and linkage contributions to differences among breed groups.

Introduction

Crossbreeding in the commercial beef cattle industry has been accepted largely because of the dual advantage of hybrid vigor and complementarity and their associated economic benefits. Crossbreeding can combine desirable characteristics from two or more breed resources into an individual commercial animal. Through the formation of new gene combinations, crossbreeding can also generate a greater degree of heterozygosity in the cross than the average of the parental breeds. The primary role of rotational crossbreeding is that it allows for the production of crossbred replacement females within the system. In addition to the exploitation of maternal heterosis as a result of using crossbred females, these females are reared in the same environment in which they are expected to perform. Dickerson (1969) cautioned that, besides the consideration of the genetic effects for the implementation of any crossbreeding program, the reproductive rate of the species and the importance of the interactions of these genetic effects with managemental and (or) marketing conditions should also be of prime concern.

The effects of crossing two or more breeds have been shown to be a function of the gene frequency differences among the loci and the degree of intra- and inter-loci gene interactions controlling the trait under consideration in the crossbred individual (Willham, 1970; Kacser and Burns, 1981; Falconer, 1982; Willham and Pollak, 1985). In other words, the magnitude of hybrid vigor generated by a given cross for a specific trait under a specified set of environmental conditions depends on the degree of relationship between the breeds involved in the cross (Damon et al., 1961; McDonald, 1972). The level of performance of straightbred offspring may also influence the magnitude of the heterotic effects since their estimation is a function of the straightbred performance (McDonald, 1972). Certain traits manifest greater heterotic value than others, particularly the preweaning and reproductive traits, probably because of their low heritabilities and the fact that they are still under the partial influence of the maternal environment provided by the dam of the calf on which the trait is measured. In general, highly heritable traits demonstrate little or no hybrid vigor. In fact, the focus of crossbreeding is on those economically important traits that are slow to improve using selection techniques.

Evaluation of the magnitude of the direct and maternal additive and nonadditive genetic effects attributable to the different breed resources available to a cattle producer should provide a better understanding of the biology of the crossbred individual. This knowledge will enhance the accuracy of prediction of the performance of different mating types to be included in a given production system. It would also lead to the increased efficiency of production of crossbred animals based on the effectiveness in the choice of breeds to be used as sires and (or) dams in any mating scheme. The selection of breeds entering and (or) the altering of the mating sequence of sire breeds in any rotational system can also be easily performed.

The objectives of this study were:

1. Estimate the direct and maternal additive and heterotic genetic effects for preweaning traits of four breeds of beef cattle.
2. Apply these genetic estimates to the prediction of preweaning performance of various breed groups under different mating systems.
3. Compare realized heterosis based on the advantage of the crossbred individual over the straightbred contemporaries with overall expected heterosis derived as a function of the estimated heterotic genetic effects for the preweaning traits.
4. Determine the importance of epistatic and (or) recombination loss effects on the preweaning performance of rotational crosses.

CHAPTER I

Literature Review

Introductory Background

Crossbreeding studies have been and are currently being carried out in different parts of the world and with different species or breeds of livestock and laboratory animals. A review of scientific literature in this area has been summarized for poultry (Sheridan and Randall, 1977; Sheridan, 1980, 1981), sheep (Nitter, 1978), swine (Sellier, 1976), dairy (Turton, 1981) and beef cattle (Mason, 1966; Cundiff, 1970; Sheridan, 1981).

The work of Winters (1952) probably established the foundation for the use of rotational crossing systems in livestock. He set out to evaluate the importance of crossing breeds of swine for their market production and to determine the value, if any, of retaining crossbred females as future parents. Dickerson (1969, 1973) and Hill (1971) presented the theoretical basis for the exploitation of crossbreeding for increased commercial livestock production.

Cartwright (1970) suggested that the efficiency of beef production could be increased more rapidly by utilizing the existing variation among breeds than by selecting within breeds for many generations. This could be attributed partly to the nonadditive genetic variability in the crosses and partly to the larger difference in gene frequency at various loci affecting economically important traits among breeds than within breeds. Dickerson (1949) proposed that controlled crossbreeding could improve the efficiency of livestock production above the levels that are achievable through selection. However, a combination of an effective selection scheme, good management and an efficient mating system is necessary to generate economic benefits from crossbreeding. Knapp et al. (1949), in a study of the potential of systematic crossbreeding, and Kincaid (1962), in a summary of crossbreeding research in the Gulf Coast region, concluded that crossirg of beef cattle breeds generated hybrid vigor as well as improvement in the efficiency of beef production.

In livestock production the primary goal of an outcrossing system is to take advantage of heterosis and complementation. However, as a consequence of meiosis in gamete formation, the straightbred parents of crossbred individuals share a sample one-half of their chromosomes and, therefore, a sample one-half of their genes with these progeny. In other words, they transmit one-half of the advantage or disadvantage for a trait that is due to the average effects of these genes to the offspring. Most crossbreeding systems allow the assembly of favorable dominance effects at many independent loci for a specific trait (Cunningham, 1987). This heterozygous gene combination is one of the major causes of the increased expression of a specific trait over and above the average of parental populations (defined as heterosis).

Therefore, differences among breeding groups in a crossbreeding system can be explained in terms of the contributions (direct and maternal additive genetic effects) of the sire and dam breeds to the offspring performance, the interaction of these effects in the individual progeny (direct heterosis effect) and whenever possible, the indirect contribution (maternal heterosis effect) of the dam as a crossbreed to the offspring performance. The additive genetic effect is the sum of the additive gene effects for which the parental breeds differ while the heterosis effect is the sum of the dominance effects created when the two breeds are crossed (Cunningham, 1987).

The maternal contribution is the result of the dam's genes for maternal ability, her permanent maternal environmental effect as determined by the environment in which she was raised and the temporary environment in which she expresses that ability (Bruckner and Slanger, 1986). This maternal effect is different from the direct effect of the dam which is an effect due to the haploid set of genes that she transmits to her offspring. The maternal effect is generally considered as a permanent environmental effect due to the genotype of the dam on the performance of her offspring (Sellier, 1976). Koch (1972) suggested that the maternal effect may be influenced by the grandmaternal environment. The usefulness of any crossbreeding system is, therefore, based on the effective utilization of breed and heterozygosity effects for the improvement of commercially important traits.

The objective of this review was to elucidate the work that has been done to separate into components the genetic effects that are relevant to the understanding of the biological basis of heterosis as well as to the application of this knowledge in the prediction of the performance of various mating systems. To underscore this goal, this review was divided into two sections for each preweaning growth trait. One section covered the papers that have contributed to the grosso modo understanding of heterosis (hybrid vigor) as a basic denominator of crossbreeding. The other section focused on the genetic components of heterosis and breed additive effects for each of the preweaning traits under consideration.

Birth Weight

Birth weight is a primary measure of prenatal growth and is obtained when the animal is still under the direct influence of its maternal environment. Extremely heavy birth weights are associated with dystocia which is responsible for economic and biological losses to the cattle producer. There is a linear relationship between dystocia level and birth weight (Laster and Gregory, 1973; Smith et al., 1976) both within and across breeds. Also, extremely light birth weights can cause such complications as reduced calf vigor and performance and early calf mortality. The desire to minimize calving difficulty in young females and thus increase returns is one of the motivations for controlled crossbreeding.

Heterosis for Birth Weight. The absence of a significant heterosis (hybrid vigor) for birth weight has been well documented (Turner and McDonald, 1969; Chapman et al., 1970; McDonald, 1972; Sagebiel et al., 1973; Drewry et al., 1978; Gaines et al., 1978; Gray et al., 1978; Dillard et al., 1980; Trail et al., 1982; Olson et al., 1985). Other researchers have, however, reported small but often significant effects of heterosis on birth weight for certain crosses (Gaines et al., 1966; Crockett et al., 1978; Gregory et al., 1978b; Comerford et al., 1987).

Pahnish et al. (1969), in a study involving Angus, Hereford, Charolais and Brown Swiss breeds, reported significant heterosis effects on birth weight and a greater heterosis effect from the Charolais crosses than was reported by Sagebiel et al. (1973). Smith et al. (1976) also noted that Charolais crosses had larger birth weights and more dystocia than the other crosses studied. Crossbred calves were found to have a 1.1 to 1.2 kg (2.9 to 3.8 %) greater birth weight than straightbred contemporaries (Gregory et al., 1965; Pahnish et al., 1969) for Angus, Hereford and Charolais crosses; a .9 (3.1 %) kg difference (Long, 1973; Gregory et al., 1978b) for Angus and Hereford crosses and a .46 kg difference (Comerford et al., 1987) relative to the crosses from Hereford, Brahman, Limousin and Simmental breeds.

McCormick and Southwell (1957) observed that Brahman-Hereford calves had heavier ($P<.01$) birth weights than Angus-Hereford calves. Kincaid (1962) found that crosses between British and Brahman type cattle were 2.7 kg heavier at birth than other crosses examined. Birth weights of F1 Brahman-Hereford and Brahman-sired crossbred calves were 3.3 and 3.5 kg, respectively, greater than those of contemporary straightbreds (Cartwright et al., 1964; Turner and McDonald, 1969). Cartwright et al. (1964) showed that Brahman x Hereford crosses exhibited large levels of heterosis for birth weight. Brown et al. (1967), studying birth weights of calves produced from matings involving Charolais, Hereford, Brahman, Angus and other breeds of cattle, found that Brahman bulls when mated to Hereford cows produced the largest percentage heterosis (22 %).

Gregory et al. (1979) observed a 5.2 kg difference in birth weight between Brahman crosses and Hereford-Angus crosses. Kidder and Chapman (1952) reported that progeny from Brahman-Angus, Brahman-Devon and their reciprocals were superior in birth weight to the straightbred lines of these crosses. Calves out of crossbred dams with predominantly

Brahman breeding tended to have small and negative heterosis effects for birth weight (Kincaid, 1962; Tucker, 1985). This result was attributed to the physiological restrictions imposed on prenatal growth of calves by the Brahman type cows. Franke (1980), reviewing heterosis on Zebu type cattle, found that heterosis for birth weight averaged 3.3 kg for F1 cross calves and 1.9 kg for calves from F1 cows.

Various workers reported percent heterosis values ranging from .0 to 4.5 for birth weight when Angus and Hereford breeds were crossed (Gerlaugh et al., 1951; Godbey et al., 1959; Kincaid, 1962; Gregory et al., 1965; Gaines et al., 1966; Pahnish et al., 1969; Sagebiel et al., 1973; Long and Gregory, 1974). The Hereford breed was found to contribute more than Angus to heterosis for birth weight, with Hereford and Shorthorn crosses generating the largest heterotic response (Damon et al., 1961; Gregory et al., 1965; Gaines et al., 1966; Rollins et al., 1969). Rollins et al. (1969) reported unweighted means of hybrid vigor for birth weight from three different stations for two-breed crosses involving Angus-Hereford (.5 kg), Hereford-Shorthorn (2.0 kg) and Angus-Shorthorn (.4 kg). Ellis et al. (1965), working with Hereford and Brahman cattle, obtained estimates of heterosis for birth weight for F1 cross calves (10.8 %), backcross calves (5.5 %) from F1 cows and backcross calves (8.2 %) from straightbred cows. Firstcross calves from Hereford dams sired by Brahman bulls were 5.5 kg heavier than Herefords whereas F1 Hereford-Brahman calves were consistently heavier (.9 kg) at birth than Brahman calves. Turner (1973) consistently ranked three-breed cross, backcross, singlecross and straightbred calves in that order within each breed of sire for birth weight. These results indicated the presence of heterosis effects for birth weight in backcross and three-breed cross calves. This influence is due partly to the heterosis in the calf and in the dam of the calf.

Crockett et al. (1978) analyzed birth weights of Angus, Brahman, Hereford and two-breed rotation crosses over three generations. Heterosis estimates for birth weight averaged over generations were 15 % (P<.01) for Angus-Brahman, 14 % (P<.01) for Brahman-Hereford and -3 % for Angus-Hereford crosses. Heterosis levels for birth weight for Angus-Brahman (12, 19, 15 %, P<.01), Brahman-Hereford (11, 13, 19 %, P<.01) and Angus-Hereford (-3, -3, -2 %) crosses, respectively, were obtained for generations one to three. Heterosis levels, pooled over all crosses for birth weight, were 7, 10 and 11 %, respectively, for generations one to three, with an average of 9 percent. Heterosis values for Brahman crosses were highly significant and positive, with an average over generations of 14.5 percent. These results indicated that heterosis for birth weight was absent for the Angus and Hereford rotational crosses but present for the British-Brahman crosses, reflecting the divergence among the British and Brahman breeds. Neville et al. (1984) evaluated two- and three-breed rotational crossbreeding experiments involving grade Angus, Hereford and Santa Gertrudis type cattle for three generations. The two-breed rotations were -1.3, 1.2 and 5.3 percent and the three-breed rotations were 1.9, 4.8 and 5.7 percent above the midparent value for generations one to three, respectively. These results tended to suggest increases in heterosis with advancing generations.

Heterosis due to the dam of the calf was generally not significant for birth weight (McDonald, 1972; Olson et al., 1985). Cartwright et al. (1964) reported a 10.8 and 8.2 percent heterosis, respectively, for F1 cross calves and backcross calves from F1 cows. These results suggested the possible existence of negative heterosis for maternal influence on birth weight as indicated by the 8.2 vs 10.8 difference, assuming that the direct and maternal heterosis effects are independent. McDonald and Turner (1972) reported small heterosis effects on birth weights of calves nursing Brahman-Angus and Brahman-Hereford dams. Heterosis values for birth weight due to the crossbred dam of the calf have been reported, ranging from 1.4 to 1.7 percent (McDonald, 1972; Cundiff, 1973b; Knapp et al., 1980). Gaines et al. (1978) observed significant differences in birth weight between crossbred and straightbred cows only when cow weight was not included as a covariate. It was suggested that cow size and heterosis could possibly be responsible for birth weight differences. Heterosis estimates evaluated for various F1 Brahman cross cows ranged from 1.6 to 2.9 kg for Brahman-Hereford (Cartwright et al., 1964; Babcock, 1978; Crockett et al., 1978) and from .8 to 3.2 kg for Brahman-Angus breed combinations (Babcock, 1978; Crockett et al., 1978).

Genetic Effects on Birth Weight

Direct and Maternal Additive Breed Effects. Direct and maternal additive genetic effects on birth weight are summarized in table 1. Because of linear dependencies in the regression model for the estimation of direct and maternal additive genetic effects, different mathematical restrictions have been employed such as deviating one breed (reference breed) from the other breeds in the model. For example, Koger et al. (1975) evaluated genetic effects using the regression method whereby the Shorthorn additive genetic effect was deviated from that of the Brahman.

Angus direct additive effects generally decreased birth weight more ($P<.01$) than that of Hereford (Gregory et al., 1978b; Vaamonde and Franke, 1984; Koch et al., 1985; Olson et al., 1985; Morris et al., 1986; Wyatt and Franke, 1986). There were no significant differences between Angus and Hereford breed maternal additive effects for birth weight. Olson et al. (1985) and Wyatt and Franke (1986) reported highly significant maternal additive genetic effects

TABLE 1. DIRECT AND MATERNAL ADDITIVE GENETIC EFFECTS FOR BIRTH WEIGHT

Source	Breed deviation	Additive direct (kg)	Additive maternal (kg)
Gregory et al., 1978b	A-H	-4.6*	.3
Alenda et al., 1980	A	-1.5	.4
	C	6.6	-1.6*
	H	-5.1	1.2
Dillard et al., 1980	A-H	-4.3	1.1
	C-H	3.4	2.5
Neville et al., 1984	A-PH	-1.2	-1.7**
	SG-PH	4.4	-2.1**
Vaamonde & Franke, 1984	H-A	5.9**	-1.3
	B-A	8.1**	-6.8**
Koch et al., 1985	A-H	-1.3**	-.1
Morris et al., 1986	A-H	-1.6**	-.1
Roberson et al., 1986	B-H	4.6**	-7.5**
Wyatt & Franke, 1986	H-A	2.6**	.1
	B-A	7.4**	-6.1**
	C-A	12.7**	-2.6**
Comerford et al., 1987	B	2.6	-6.7**
	H	-1.8	2.3*

*P<.05.
**P<.01.
A = Angus, B = Brahman, C = Charolais, H = Hereford, PH = Polled Hereford, and SG = Santa Gertrudis.

(4.6 to 4.8 kg) for birth weight of Brown Swiss deviated from Angus. Spelbring et al. (1977) also reported similar results when comparing the Angus and Milking Shorthorn. These results suggest the positive influence of in utero maternal environment of dairy type breeds. Neville et al. (1984) observed negative additive genetic effects of Angus on birth weight for all three generations which decreased in magnitude and level of significance as generations advanced. Also, Angus maternal additive influence relative to Polled Hereford was generally negative and significant during each generation. These facts tend to confirm the claim that Angus sires and dams generally produce lighter calves at birth.

A larger, positive direct additive effect of the Brahman breed relative to Angus and Hereford in contrast to the negative Brahman maternal additive influence ($P<.01$) on birth weight was reported in the literature (Vaamonde and Franke, 1984; Roberson et al., 1986; Wyatt and Franke, 1986). Roberson et al. (1986) found that the largest of the estimated genetic effects on birth weight was the Brahman-Hereford maternal additive deviation. The similarity among birth weights of all mating combinations involving Brahman dams was partially explained by the size of this maternal effect. Comerford et al. (1987) obtained a negative ($P<.01$) Brahman maternal additive influence on birth weight based on a diallel design analysis. These results support the evidence that Brahman type females generally gave birth to smaller sized calves than other female breeds of equal mature size when mated to similar sire breeds. Brahman sires, however, produced larger sized calves at birth than other sire breeds when mated to similar size non-Brahman type females.

The Charolais direct additive effect tended to increase birth weight (Alenda et al., 1980; Dillard et al., 1980; Wyatt and Franke, 1986) whereas its maternal additive influence decreased birth weight. Sagebiel et al. (1973) found no difference between the maternal effects of Charolais and Angus whereas Dillard et al. (1980) observed a slightly positive (1.4 kg) difference in favor of the Charolais breed. Neville et al. (1984) obtained a 2.1 kg larger ($P<.01$) Polled Hereford maternal additive breed effect than that of Santa Gertrudis for birth weight when averaged across generations. Significant total maternal (maternal plus grandmaternal) effects on birth weight were negative for Charolais but positive for Angus and Hereford breeds (Alenda et al., 1980). Alenda et al. (1980) and Comerford et al. (1987) reported negative direct and positive maternal additive influences of the Hereford breed on birth weight. Although maternal effects accounted for some increase in birth weight (Comerford et al., 1987), the direct and maternal effects for Hereford tended to negate each other.

These results suggest the importance of the contributions of breeds as sires and (or) dams to the birth weight of the offspring produced by crossing such breeds. The genetic differences among breeds for birth weight suggest the possibility of controlling this trait through the use of breed complementarity.

Direct and Maternal Heterosis Effects. Estimates of these effects were adapted from various sources and are presented in table 2. These estimates represent the deviation of the average performance of the F1 cross from the average of their parental breeds and were calculated as deviations from zero. The Brahman breed crossed with British breeds (Angus and Hereford) demonstrated the largest direct heterosis effect on birth weight (Vaamonde and Franke, 1984; Roberson et al., 1986; Wyatt and Franke, 1986; Comerford et al., 1987). Maternal heterosis estimates for birth weight ranged from .3 to 1.0 kg (Vaamonde and Franke, 1984; Wyatt and Franke, 1986) for Angus-Brahman and from .6 to 1.8 kg (Vaamonde and Franke, 1984; Roberson et al., 1986; Wyatt and Franke, 1986) for Hereford-Brahman combinations.

Direct and maternal heterosis effects on birth weight were generally small (-3.2 to 1.3 and -1.3 to 1.5 kg, respectively) for crosses among British (Angus-Hereford) breeds (Gregory et al., 1978b; Alenda et al., 1980; Dillard et al., 1980; Knapp et al., 1980; Vaamonde and Franke, 1984;

TABLE 2. DIRECT AND MATERNAL HETEROSIS EFFECTS FOR BIRTH WEIGHT

Source	Breed combinations	Direct heterosis (kg)	Maternal heterosis (kg)
Gregory et al.,1978b	AH	1.3**	
Alenda et al., 1980	AH	-3.2	-1.3
	AC	.5	.6
	CH	3.0	.2
Dillard et al., 1980	AH	.5	
	AC	1.1	
	CH	.7	
Knapp et al., 1980	AH		-.2
	AC		.7
	CH		.3
Neville et al., 1984	APH	.2	
	ASG	1.2*	
	PHSG	.8	
Vaamonde & Franke, 1984	AH	1.2**	1.5**
	AB	3.5**	.3
	BH	2.3**	1.8**
Koch et al.,1985+	AH	.8**	1.0*
Morris et al., 1986+	AH	.7**	1.3**
Roberson et al., 1986	BH	2.2**	.6*
Wyatt & Franke, 1986	AH	.2*	-.9**
	AB	2.9*	1.0**
	AC	-1.7**	1.0**
	BC	-.3	
	BH	2.9**	.8**
	CH	-1.7**	1.8**
Comerford et al., 1987	BH	2.6	

*P<.05.
**P<.01.
A = Angus, B = Brahman, C = Charolais, H = Hereford, PH = Polled Hereford, and SG = Santa Gertrudis.
+Heterosis effects were adjusted for additive by additive effects.

Koch et al., 1985; Morris et al., 1986; Wyatt and Franke, 1986). Koch et al. (1985) and Morris et al. (1986), using various mating types and correcting dominance for additive by additive epistatic effects, found significant direct and maternal heterotic responses for birth weight due to Angus-Hereford crosses. When epistatic effects were ignored, maternal heterosis estimates ranged from .5 (Koch et al., 1985; $P<.05$) to 1.5 kg (Morris et al., 1986; $P<.01$).

Most researchers have reported direct and maternal heterosis estimates of the Charolais crossed with British breeds for birth weight to be nonsignificant (Alenda et al., 1980; Dillard et al., 1980; Knapp et al., 1980). However, Wyatt and Franke (1986) obtained negative direct and positive maternal heterotic genetic effects ($P<.01$) of Charolais-British crosses for birth weight from the analysis of data collected from different mating types across the Southern region. Brahman-Charolais crosses had a negative ($P<.05$) direct heterosis effect on birth weight. Neville et al. (1984) observed significant direct heterotic effects on birth weight associated with crosses involving Angus, Polled Hereford and Santa Gertrudis breeds in generation one of a three-generation rotational crossbreeding study. These effects tended to be small when averaged over all crosses and generations. Average maternal heterosis effects were negative ($P<.01$) for the first and positive for the second ($P<.01$) and third generations. It was noted that the direction of heterosis effects on birth weight was not repeatable across generations.

These findings suggested the importance of the contributions of the heterotic genetic effects to the variation in birth weight in the calf per se (direct effects) and the cow of the calf (maternal effects) as an environmental component. This contribution has also been demonstrated to be a function of specific breed combinations and the degree of breed heterozygosity involved in the cross.

Preweaning Average Daily Gain

Preweaning growth rate (ADG) provides a good indicator of the early postnatal growth and of the maternal contribution to this growth. This trait is, therefore, a function of both the genetic potential of the individual calf to grow from birth to weaning and of the maternal ability of the calf`s dam.

Heterosis for ADG. Many workers have illustrated the significance of heterosis for preweaning gain (Gregory et al., 1965, 1978a, b; Gaines et al., 1966; Smith et al., 1976; Tucker, 1985; Roberson et al., 1986). The significant interaction of breed of sire by breed of dam on ADG and weaning weight has been interpreted to reflect the relatively low growth response of Jersey- and Angus-sired crossbred calves to the increased milk production of the Angus dams (Smith et al., 1976). On the other hand, Gregory et al. (1978a) suggested that this interaction was indicative of the greater response of crossbred calves sired by breeds transmitting higher growth potential to the increased maternal ability, especially milk yield, of the Angus dams. Gregory et al. (1978b) also suggested that it reflected the importance of heterosis and reciprocal cross differences for preweaning traits. Most other researchers suggested that this interaction was evidence of the significant contribution of heterosis to increased prenatal and postnatal preweaning growth rate (Cartwright et al., 1964; Gregory et al., 1965; Klosterman et al., 1968; Pahnish et al., 1969; Smith et al., 1976).

Differences between crossbred and straightbred calves for preweaning ADG reported in the literature ranged from .03 to .05 kg per day (Gregory et al., 1965; Long, 1973; Long and Gregory, 1974; Gregory et al., 1978b). Other workers gave estimates of heterosis averaged over both sexes for daily gain ranging from 1.7 to 4.8 percent (Gregory et al., 1965; Gaines et al., 1966; Sagebiel et al., 1967; Pahnish et al., 1969). Long (1980), in a comprehensive review of crossbreeding research, obtained a weighted heterosis percentage for preweaning gain of 4 percent (.3 to 8 %).

Angus and Hereford crossbred calves outgained the straightbreds from birth to weaning by .03 to .05 kg/d (Gerlaugh et al., 1951; Kincaid, 1962; Long and Gregory, 1974; Smith et al., 1976). Kincaid (1962) found small differences between the F1 British cross, backcross and three-breed cross calves for preweaning ADG with an average heterosis of 5 percent. Gregory et al. (1965) obtained nonsignificant heterosis estimates for two-way (AH, HS and AS) crosses of the British breeds. However, when these crossbreds were compared to the superior parent on weaning weight basis, significant differences in preweaning gain were found for Hereford-Angus (.03 kg) and Hereford-Shorthorn (.05 kg) crosses. Gaines et al. (1966) reported significant heterosis levels for all F1 calves (.10 to .16 kg) except for Angus-Hereford (-.02 kg) and Shorthorn-Hereford (-.16 kg) when studying Angus, Hereford and Shorthorn crosses. The three-breed crosses produced about one-half as much heterosis as the F1 crosses and the backcrosses had no significant heterosis for preweaning gain. They observed that significant heterosis estimates occurred whenever crossbred calves were suckling Angus or Shorthorn cows. Gregory et al. (1965) and Long and Gregory (1974) both reported that Hereford-Angus calves gained about .06 kg more per day than their reciprocals.

Hereford-sired crossbred calves generally showed the greatest amount of heterosis for preweaning ADG (Gregory et al., 1965; Gaines et al., 1966; Long and Gregory, 1974; Tucker, 1985). Neville et al. (1984), using Angus, Polled Hereford and Santa Gertrudis breeds in a three generation rotational crossing experiment, found that the two- and three-breed rotation crosses, with the exception of Angus-Santa Gertrudis in generation one, exceeded ($P<.01$) the parental means during each generation. The three-breed rotations also exceeded the average of the two-breeds in ADG during each generation.

Kincaid (1962) reported that crossbred calves produced by crossing Brahman with British breeds of cattle surpassed their straightbreds by .07 kg in average daily gain. Brahman-Hereford calves sired by Brahman bulls gained .09 kg more per day than Hereford calves whereas calves sired by Charolais bulls gained .05 kg more daily than any of the crossbreds. Reimer and Cobb (1971), evaluating crosses from Angus, Hereford and Charolais cattle for ADG to weaning, found that the crossbred calves generally maintained a fairly consistent advantage over the straightbreds. Gregory et al. (1979) reported that Brahman crosses had significantly higher preweaning gain than those of Sahiwal (.042 kg/d) and Pinzgauer (.031 kg/d) for sire breed group comparisons. Hereford-Angus reciprocal crosses were less (-.03 kg/d, $P<.01$) than Brahman crosses for gain to weaning. Smith et al. (1976) reported the superiority of Charolais crosses in preweaning ADG. Tucker (1985) noted that Charolais-sired two-breed rotation calves for the first and third generations of the rotational crossbreeding data that will be used in this study had lower estimates of heterosis for ADG than Angus- and Hereford-sired calves.

Effects of heterosis due to the calf nursing a crossbred dam were found to differ significantly between specific crosses for preweaning growth traits (Cundiff, 1973b). Ranking these effects for ADG relative to the two-way crosses among British breeds, he obtained 7.7 (.06 kg, $P<.01$), 4.6 (.04 kg, $P<.01$) and 2.4 (.02 kg, $P<.05$) percent heterosis, respectively, for Hereford-Shorthorn, Hereford-Angus and Angus-Shorthorn reciprocal crosses. A similar ranking of F1 calves of British breeds for preweaning gain was observed by Gregory et al. (1965), suggesting that Angus and Shorthorn breeds are more similar in genotype to each other than they are to the Hereford breed. Notter et al. (1978) evaluated preweaning growth of progeny produced by mating Angus, Charolais, Hereford, Jersey, South Devon, Simmental and Limousin bulls to Angus and Hereford cows. They found that while the progeny of Jersey and Simmental cross cows grew fastest (.79 kg/d) when averaged over ages, those of Hereford-Angus cross cows grew least rapidly (.72 kg/d) to weaning.

Knapp et al. (1980) reported that Hereford-Angus, Hereford-Charolais and Angus-Charolais crosses tended to gain faster from birth to weaning than their reciprocals. However, these same crosses as dams produced slower gaining calves. Leonard et al. (1967) reported a similar relationship between the performance of reciprocals as calves and subsequently as dams. This trend is suggestive of the hypothesis (Cundiff et al., 1974) that maternal environment for preweaning gain is negatively influenced by the favorable maternal effects expressed in the previous generation (Alenda et al., 1980; Alenda and Martin, 1981).

Kidder and Chapman (1952) reported that calves from Brahman-Angus, Brahman-Devon and their reciprocals gained weight faster from birth to weaning than the straightbreds. Roberson et al. (1986), working with Brahman, Hereford and F1 cross cattle, also reported that calves from F1 Brahman-Hereford cows had the largest gains from birth to weaning based on comparisons within sire breed types (straightbred vs F1 cross sires). Brahman dams tended to produce calves with greater preweaning gains than Hereford dams when mated to either F1 cross or Hereford sires. However, when mated to Brahman sires, the Brahman dams had calves with lower gains than did Hereford dams. These results tend to suggest that heterosis in the calf is more important than maternal effects.

Genetic Effects on ADG

Direct and Maternal Additive Breed Effects. Table 3 contains the direct and maternal additive genetic effects for preweaning ADG adapted from different sources. Gregory et al. (1978b) reported the advantage (.05 kg/d, P<.01) of Angus over Hereford in additive breed effect for ADG in

TABLE 3. DIRECT AND MATERNAL ADDITIVE GENETIC EFFECTS FOR PREWEANING AVERAGE DAILY GAIN

Source	Breed deviation	Additive direct (kg)	Additive maternal (kg)
Gregory et al., 1978b	A-H	.05*	.04*
Dillard et al., 1980	A-H	.02	.04**
	C-H	.08*	.13**
Vaamonde & Franke, 1984	H-A	.06	-.06**
	B-A	-.02	.03*
Koch et al., 1985	A-H	-.02**	.05**
Morris et al., 1986	A-H	.001	.012**
Roberson et al., 1986	B-H	-.02**	.02**
Wyatt & Franke, 1986	H-A	-.00	-.04**
	B-A	-.02**	.05**
	C-A	.12**	.03

*P<.05.
**P<.01.
A = Angus, B = Brahman, C = Charolais, and H = Hereford.

contrast to that of Hereford over Angus reported by Koch et al. (1985). Vaamonde and Franke (1984) obtained a large but nonsignificant direct additive genetic difference between Hereford and Angus relative to gain from birth to weaning.

The Angus maternal additive genetic effect relative to Hereford for ADG was significant and positive for most of the studies (Gregory et al., 1978b; Dillard et al., 1980; Vaamonde and Franke, 1984; Koch et al., 1985; Wyatt and Franke, 1986). Morris et al. (1986) observed, however, that with birthdate in the model as a covariate, the Hereford direct additive genetic effect exceeded that of Angus for ADG by .03 kg per day (P<.01). The Angus maternal additive genetic effect increased ADG by .008 kg more (P<.01) than that of Hereford with birthdate as a covariate and .012 kg per day without the covariate.

Neville et al. (1984), working with rotational crossbreeding data, found that the direct additive genetic difference in ADG between Angus and Polled Hereford breeds favored (P<.01) the Polled Hereford in generation three. They reported an average across three generations of .021 kg (P<.05) in favor of the Polled Hereford breed. However, the maternal additive difference between Angus and Polled Hereford increased with advancing generations and became highly significant and positive in generation three, with an average of .031 kg (P<.01) in favor of the Angus. Although the Hereford breed apparently transmitted a large direct genetic effect for calf preweaning growth, the Hereford maternal additive effect, expressed mainly through milk production (Notter et al., 1978), was lower than that of the Angus. The Angus direct and maternal additive genetic effects were less ($P<.01$) than those of Brown Swiss by .11 and .13 kg per day for preweaning ADG (Olson et al., 1985).

The Brahman direct additive genetic effect on gain was less ($P<.01$) than that of Hereford (Roberson et al., 1986) and that of Angus (Wyatt and Franke, 1986). However, the Brahman maternal additive effect on ADG was more ($P<.01$) than that of Hereford (Roberson et al., 1986) and that of Angus (Vaamonde and Franke, 1984; Wyatt and Franke, 1986). Roberson et al. (1986) suggested that the advantage of the Brahman maternal additive effect over that of the Hereford breed explained the greater preweaning gains of the crosses from Brahman dams. The influence of the larger Hereford direct additive effect was evident in the greater preweaning gains of the Hereford-sired calves from F1 or Brahman dams.

Wyatt and Franke (1986) reported a .12 kg direct additive effect of the Charolais relative to Angus for preweaning ADG compared to the .064 kg Charolais direct additive effect relative to Hereford and Angus reported by Notter et al. (1978) and the .06 kg Charolais direct additive effect relative to Angus reported by Dillard et al. (1980). Wyatt and Franke (1986) found a positive (.03 kg) maternal additive genetic effect for the Charolais as deviated from the Angus, whereas Notter et al. (1978) found a negative (-.017 kg) effect for the Charolais as deviated from Hereford and Angus. Dillard et al. (1980) reported a highly significant maternal additive difference (.09 kg/d) for Charolais over Angus for preweaning gain. Neville et al. (1984) found that the Santa Gertrudis additive direct effect on gain was more (P<.01) than that of Polled Hereford over three generations of a rotational crossbreeding study, with an average of .082 kg (P<.01). Similarly, the Santa Gertrudis maternal additive effect was .089 kg more (P<.01) than that of Polled Hereford over all generations. These results reflect the growth advantage and the mothering ability, primarily milk production, of the Charolais breed (Melton et al., 1967; Notter et al., 1978).

Direct and Maternal Heterosis Effects. These effects were adapted from different sources and summarized in table 4. Generally positive and significant Angus-Hereford direct and maternal heterosis effects on daily gain from birth to weaning have been observed (Gregory et al., 1978b; Dillard et al., 1980; Knapp et al., 1980; Vaamonde and Franke, 1984; Wyatt and Franke, 1986). Neville et al. (1984) reported positive and significant direct heterosis effects on ADG for Angus-Polled Hereford crosses for generation three, with an average over generations of .051 kg (P<.01) per day. Average maternal heterosis for Angus-Hereford crosses reported for ADG was .02 (Dillard et al., 1980, P<.01) and

TABLE 4. DIRECT AND MATERNAL HETEROSIS EFFECTS ON PREWEANING AVERAGE DAILY GAIN

Source	Breed combinations	Direct heterosis (kg)	Maternal heterosis (kg)
Gregory et al., 1978b	AH	.026**	
Dillard et al., 1980	AH	.03**	
	AC	.01	
	CH	.05*	
Knapp et al., 1980	AH		.019
	AC		-.027
	CH		.015
Neville et al., 1984	APH	.051**	
	ASG	.033*	
	PHSG	.102**	
Vaamonde & Franke, 1984	AH	.02*	.03**
	AB	.10**	.09**
	BH	.11**	.13**
Koch et al., 1985+	AH	.031**	.057**
Morris et al., 1986+	AH	.005**	.014**
Roberson et al., 1986	BH	.02**	.02**
Wyatt & Franke, 1986	AH	.02**	.022**
	AB	.10**	.052**
	AC	.005	.023*
	BH	.099**	.081**
	BC	.089**	
	CH	.01	.028**

*P<.05.
**P<.01.
A = Angus, B = Brahman, C = Charolais, H = Hereford, PH = Polled Hereford, and SG = Santa Gertrudis.
+Heterosis effects have been adjusted for additive by additive epistatic effects.

.023 (Neville et al., 1984; P<.05) kg per day, respectively. Koch et al. (1985) and Morris et al. (1986) estimated AH direct and maternal heterosis effects for ADG by adjusting the dominance effects for additive by additive epistatic effects. They found these estimates to range from .01 to .03 kg for direct and .014 to .06 kg for maternal heterosis effects for gain. Maternal heterosis estimates for daily gain to weaning unadjusted for epistatic effects ranged from .012 (Morris et al., 1986) to .06 (Koch et al., 1985; P<.01) kg per day. Olson et al. (1985) reported .04 kg (P<.01) maternal heterosis estimate for Angus-Brown Swiss crosses for preweaning gain.

Brahman crosses exhibited positive and significant direct heterosis effects for preweaning gain (Vaamonde and Franke, 1984; Roberson et al., 1986; Wyatt and Franke, 1986). Brahman-British crosses demonstrated positive and significant maternal heterosis effects on gain (Vaamonde and Franke, 1984; Roberson et al., 1986; Wyatt and Franke, 1986). Roberson et al. (1986) explained that Brahman-Hereford calves had greater preweaning gains than did straightbred Brahmans because of the direct heterosis value in the crossbred calves and the one-half larger Hereford additive contribution. However, straightbred Hereford calves had the smallest gains probably because of the relatively low Hereford maternal ability which outweighed the Hereford direct additive advantage.

Wyatt and Franke (1986) obtained a large, positive ($P<.01$) direct heterosis effect of Charolais-Brahman crosses for preweaning gain. Wyatt and Franke (1986) reported that direct heterosis effects of Charolais-Angus and Charolais-Hereford combinations were not significant for ADG. Dillard et al. (1980) reported a similar estimate for Charolais-Angus but a larger ($P<.05$) and positive value for Charolais-Hereford.

Positive and significant maternal heterosis effects in Charolais-British crosses for preweaning gain have been observed (Wyatt and Franke, 1986). Knapp et al. (1980) reported negative Charolais-Angus and positive Charolais-Hereford maternal heterosis values for preweaning daily gain. Neville et al. (1984) reported positive direct heterosis in Angus-Santa Gertrudis (.033 kg/d, $P<.05$) and Polled Hereford-Santa Gertrudis (.102 kg/d, $P<.01$) breed combinations for gain.

Weaning Weight

Weaning weight is a composite trait of birth weight and preweaning ADG and age at weaning (Peacock et al., 1978). It is an economically important trait in beef cattle and directly relates to the value of the calf at weaning, especially in Louisiana where most of the calves produced are sold as feeder calves. Weaning weight is a phenotypic expression of the calf. It is influenced by the direct and maternal genetic effects of the calf and of the dam, respectively. The low to moderate heritability of this trait (Preston and Willis, 1974; Woldehawariat et al., 1977), the relatively low reproductive rate of cattle, the long generation interval and the relatively low selection differentials make the traditional intrabreed phenotypic selection for greater weaning weights a slow method of breed improvement (Chapman et al., 1969; Koch et al., 1974; Nwakalor et al., 1976). Improvement in weaning weight is a function of increased preweaning growth potential and of improved maternal ability (Bruckner and Slanger, 1986).

Heterosis for Weaning Weight. Percentage heterosis for weaning weight ranged from 2.1 to 7.2 (Gerlaugh et al., 1951; Gregory et al., 1965; Gaines et al., 1966; Mason, 1966; Sagebiel et al., 1967, 1974; Pahnish et al., 1969; Rollins et al., 1969; McDonald and Turner, 1972; Long and Gregory, 1974; Smith et al., 1976; Drewry et al., 1978; Bailey, 1981). Long (1973) reported an average heterosis of 5 (3 to 16 %) percent for weaning weight. Koger et al. (1975) reported a 14 to 32 percent advantage of crossbred calves over the straightbreds for weaning weight. Various estimates of heterosis ranging from 3.8 to 31.9 kg were reported for weaning weight (Damon et al., 1961; Gregory et al., 1965, 1978b; Long and Gregory, 1974; Drewry et al., 1978; Gaines et al., 1978; Peacock et al., 1978).

Angus-Hereford and reciprocal crosses were heavier at weaning than the straightbreds (Gerlaugh et al., 1951).

Gregory et al. (1965) found a difference of 12.8 and 14.0 kg, respectively, for Hereford-Angus and Hereford-Shorthorn reciprocals, while that between the Angus-Shorthorn reciprocals was 1.7 kg for weaning weight. Gregory et al. (1978b) observed an 11.8 kg difference ($P<.01$) between Hereford-Angus and reciprocals for weaning weight. There was a large difference in weaning weight for the reciprocal crosses involving the Hereford breed, probably due to the low maternal ability of the Hereford cow and the positive growth effects transmitted by the Hereford sire.

Damon et al. (1961) reported heterotic effects due to Angus-Hereford crosses of -4.6 kg for 180 day weight. Gregory et al. (1965) reported that the estimate of heterosis for weaning weight was almost twice as great for the Hereford-Angus (9.9 kg) and Hereford-Shorthorn (10.8 kg) calves as for the Angus-Shorthorn (5.8 kg). These differences were, however, not statistically significant. Gaines et al. (1966) estimated heterosis for adjusted weaning weight of calves produced by crossing Angus, Hereford and Shorthorn cattle. Hereford-Angus, Shorthorn-Angus and Hereford-Shorthorn crosses displayed the largest heterotic response of 14.5, 13.2 and 17.6 kg, respectively, while their reciprocals showed considerably smaller increases in weaning weight. The Shorthorn-Hereford reciprocal cross calves manifested a highly negative heterosis effect of 10.0 kg for weaning weight.

Relative to weaning weight, Crockett et al. (1978) reported an overall heterosis of 5 % for Angus-Hereford crosses, while Neville et al. (1984) reported an overall heterosis of 3.5 % for Angus-Polled Hereford crosses over three generations of a rotational crossing experiment. Peacock et al. (1978) reported an overall heterosis of 7.6 % for F1 reciprocal crosses involving Angus, Brahman and Charolais cattle. Chapman et al. (1970), using data from the first and second generations of the rotational crossbreeding experiment reported by Neville et al. (1984), attributed the observed increase in heterosis effects for weaning weight as generations advance partly to the disappearance of some residual heterozygosity in the grades, primarily the Angus and Santa Gertrudis, and partly to the environmental conditions that might have varied from generation to generation.

Rollins et al. (1969) studied three two-way crosses of Angus, Hereford and Shorthorn cattle and reported heterosis estimates of 7.0 (4.5 %), 10.2 (4.5 %) and 6.5 (4.4 %) kg, respectively, for Hereford-Angus, Hereford-Shorthorn and Shorthorn-Angus calves at weaning. Heterosis due to Hereford-Angus crosses for weaning weight ranged from 6.4 to 8.5 ($P<.01$) kg (Smith et al., 1976; Gray et al., 1978; Gregory et al., 1978b). Other studies have documented considerably lower (Damon et al., 1959) and higher (McDonald and Turner, 1972; Long and Gregory, 1974) estimates of heterosis for weaning weight when crossing Angus and Hereford beef breeds. Firstcross calves out of Hereford dams were about 15 kg heavier at weaning than the straightbred Hereford calves (Cartwright et al., 1964). This was attributed to the higher growth potential of the crossbred calf. Cartwright and Carpenter (1961) observed that crossbred calves on Hereford dams nursed more frequently and for longer periods of time than did straightbred Hereford calves. Consequently, part of the advantage of crossbred calves may be ascribed to increased milk flow of the dam due to the frequent and persistent suckling stimulus of the calf.

Brahman-Hereford and Brahman-Shorthorn calves were heavier at weaning and more profitable than straightbred Hereford and Shorthorn calves (Black et al., 1934). Firstcross Brahman-British calves showed positive levels of heterosis for weaning weight of 7.0 kg for Brahman-Brangus (Damon et al., 1959, 1961), 19.4 to 26 kg for Brahman-Hereford (Damon et al., 1961; Cartwright et al., 1964) and of 16.7 to 36.6 kg for Brahman-Angus calves (Baker and Black, 1950; Damon et al., 1961; Peacock et al., 1978; Reynolds et al., 1982). Peacock et al. (1978) reported significant heterosis effects of Angus-Brahman (12.2 %) and Brahman-Charolais (7.1 %) and a nonsignificant heterosis effect of Angus-Charolais (2.1 %) crosses for weaning weight. Reynolds et al. (1982) reported that Brahman-Angus reciprocal crosses weighed 23.2 % more ($P<.01$) at weaning than the straightbreds. This level of heterosis was higher than that reported for other Brahman-British crosses (Damon et al., 1959; Cundiff, 1970) and much greater than that reported for British-British crosses (Pahnish et al., 1969; Cundiff, 1970). McCormick and Southwell (1957) observed that Brahman-Hereford calves were somewhat heavier in weaning weight than Angus-Hereford calves.

Damon et al. (1959) observed that Brahman and Brahman type dams raised calves with the greatest amount of heterosis for weaning weight. Firstcross calves raised by Brahman dams were about 8.2 kg heavier at weaning than calves of the same breeding but raised by Hereford dams. It was suggested that Brahman dams were probably more able to respond to the added stimulus of suckling of crossbred calves than Hereford dams. Brahman-sired crossbred calves were 21.2 kg heavier at weaning than their straightbred contemporaries (Turner and McDonald, 1969). Gregory et al. (1979) also observed that Brahman-sired crossbred calves were the heaviest ($P<.01$) at weaning. Franke (1980) reported a weighted average of 21.7 kg heterotic advantage of the Brahman crosses for weaning weight. This was probably more so because of the heterotic advantage of Brahman crosses than the transmitted Brahman direct effects for growth.

Crockett et al. (1978) reported an overall heterosis percentage of 17.5 due to the Brahman-Hereford and Angus-

Brahman crosses for 205 day weight over three generations of a rotational crossbreeding study. The average heterosis levels for weaning weight due to Angus-Brahman and Brahman-Hereford crosses were 17 and 18 percent, respectively. Heterosis levels averaged over all crosses were 15, 9.0 and 17 percent, respectively, for generations one to three. They found that the two-breed rotations effectively maintained relatively high levels of heterosis for the three generations.

Pahnish et al. (1969) evaluated heterosis for 205-d weight for crosses involving Angus, Charolais, Hereford and Brown Swiss breeds. Angus bulls mated to Charolais females produced the best performing crossbred calves because they surpassed all other crossbreds in preweaning gain and weaning weight and had moderate average birth weights which were uninfluenced by heterosis. Smith et al. (1976) reported that weaning weights of Charolais crosses were greater than those of Angus and Hereford crosses. Peacock et al. (1978) reported heterosis levels of 7.1 percent due to Brahman-Charolais and 2.1 percent due to Angus-Charolais crosses for unadjusted weaning weight.

McDonald (1972) analyzed records from the matings of straightbred cows of Angus, Brahman, Brangus and Hereford breeds with sires of these same breeds plus Charolais. Heterosis due to the crossbred cow but measured on the calf as an environmental effect was estimated by comparing the average performance of triplecross progeny with that of singlecross progeny from the parental breeds of the dam. Average estimated heterosis for weaning weight was 7.2 percent. Franke (1980) reported a weighted 31.1 kg estimate of heterosis due to Brahman crossed cows for weaning weight. Effects of heterosis in the dam, derived by comparing straightbred Angus, Hereford and Shorthorn cows with their crossbred half-sisters produced in generation one when both were mated to the same sires of a third breed, were 8.4 kg ($P<.01$) for 200-d weight (Cundiff, 1973b). Effects of heterosis for 200-d weight were greatest for Hereford-Shorthorn (13.1 kg, 6.8 %, $P<.01$) followed by Hereford-Angus (8.1 kg, 4.2 %, $P<.01$) and Angus-Shorthorn (4.2 kg , 2.0 %) reciprocal cross cows. Cundiff (1973b) concluded that this heterotic value is a reflection of the greater and more persistent milk production of crossbred cows relative to the straightbreds. The expression of this heterosis was found to depend on the age at which the crossbred females were first exposed to calve (2 vs 3 yr).

Cundiff (1973a) found significant differences between reciprocal cross cows in milk production at 6 weeks and at weaning; calf weight differences at 200 days between Hereford-Angus reciprocal crosses occurred in favor of Angus-Hereford females. Differences between Hereford-Shorthorn reciprocal crosses also tended to favor females out of Hereford dams; Angus-Shorthorn reciprocal differences were small and not significant for maternal effects. Calves out of Hereford-Angus dams were 12.7 kg lighter at weaning than those by the same sires out of Angus-Hereford dams. A significant interaction between maternal effects expressed in succeeding generations was evident through the results of Hereford-Angus reciprocal crosses. He found also that the Hereford-Angus females were heavier as calves, carried more condition at maturity but produced less milk and lighter calves than Angus-Hereford females.

It was noted that the tendency to fatten may be influenced by the favorable maternal environment experienced by the young calves out of Angus dams compared with Hereford dams. This was suggestive of a probable interaction between, on the one hand, the mammary and endocrine development in the growing female and, on the other, the fattening in the female calf. This interaction could likely produce a decrease in the expression of her maternal ability. Results are in general agreement with those of Koch (1972) which provided evidence that a heifer's mothering ability is negatively associated with her own dam's mothering instincts. McDonald and Turner (1972) failed to show differences in the manifestation of mothering ability between Hereford-Angus and Angus-Hereford reciprocal cross cows.

Cundiff (1973a) concluded that these findings were indicative of the greater production that can be expected from Angus-Hereford than from Hereford-Angus cows in a specialized crossing scheme involving F1 crossbred dams. It was noted, however, that these differences had no consequence in rotational crossing systems since favorable effects in one generation could be cancelled in the next generation as revealed by the complete cancellation of reciprocal effects of calf weights in Hereford-Angus and Angus-Hereford crosses. Consequently, any rotational system involving Hereford and Angus breeds can only benefit from the substantial effects of individual heterosis expressed by the crossbred calf and the maternal heterosis expressed by the crossbred cow.

Lush et al. (1930) were perhaps the first to indicate that Brahman-Hereford cows raised considerably heavier calves at weaning than did Hereford cows when mated to Hereford bulls. This advantage was attributed in large part to the good milk-producing qualities of the crossbred cows. Cartwright et al. (1964) presented evidence of heterosis in F1 Brahman-Hereford cows. Percentage advantage of Brahman-Hereford backcross calves from F1 dams was 18.8, while that of similar crossbred calves from straightbred dams was 9.3 % compared to their straightbred contemporaries. They concluded that the greater heterosis in backcross calves raised by F1 cows than in similar calves raised by staightbred cows was due to the maternal heterosis (9.5 %) expressed by the F1 cows. Calves out of F1 cows and sired by

Hereford bulls were 11.3 kg above average, while calves sired by Brahman bulls from F1 cows were 2.7 kg above average. All calves from the crossbred cows in this study were above average. Brahman crossbred cows produced the heaviest calves at weaning among the crossbred cows studied (Turner and McDonald, 1969). The heterosis effect due to Brahman-Hereford cows on weaning weight ranged from 30.7 to 34.4 kg (Cartwright et al., 1964; Turner and McDonald, 1969; Babcock, 1978; Crockett et al., 1978). Brahman-Hereford dams provided the largest estimate of heterosis for weaning weight of all the singlecross dams, while crosses involving Angus-Brangus dams produced the least (McDonald, 1972). Calves from Brahman-Hereford cows were influenced largely by additive and maternal effects.

McDonald and Turner (1972) evaluated heterosis using female crosses of Angus, Brahman, Brangus, Hereford and Charolais breeds. Brahman-Hereford cows preceded Brahman-Angus cows in the amount of heterosis expressed for weaning weight. The magnitude of the heterosis expressed by the Hereford-Angus cows was small and nonsignificant. Effects of heterosis due to Brahman-Angus dams on weaning weight ranged from 24.9 to 43.5 kg (Kidder et al., 1964; Turner and McDonald, 1969; Babcock, 1978; Crockett et al., 1978). Gaines et al. (1978) evaluated weaning weights of calves produced from crosses involving Angus, Hereford and Shorthorn breeds. Calves from crossbred cows performed significantly better than those from straightbred cows. Calves out of Angus-Hereford cows were 12.7 kg heavier at weaning than those from Hereford-Angus cows. Cundiff et al. (1974) reported similar findings, this being a reflection of the probable effect of maternal granddams. They also observed an 8.4 kg advantage of the calves from the crossbred cows over those from straightbred cows in weaning weight. McDonald (1972) reported that heterosis in the calf was more important than that in the Angus-Hereford dams expressed as an environmental effect on calf weaning weight.

Turner and McDonald (1969) reported that the greatest heterotic advantage for 205-d weight occurred with the three-breed cross, backcross and firstcross calves in that order. Angus-sired backcross calves were heavier at weaning than Angus-sired three-breed cross calves. Weaning weights of backcross calves from F1 Brahman cross cows were superior to the midparent values (Kidder et al., 1964). Babcock (1978) found that backcross and three-breed cross calves from F1 Brahman cross cows were heavier (24.9 to 34.0 kg) at weaning than the calves out of the straightbred dams. Peacock et al. (1978) reported that three-breed cross calves nursing F1 cross cows weighed 17.8 percent more at weaning than those from straightbred cows. Neville et al. (1984) obtained average cow heterosis for 205-d weight of -3.0, 17.9 ($P<.01$) and 1.4 kg, respectively, for generations one to three, with an overall average of 5.4 ($P<.05$) kg. Notter et al. (1978) observed no significant differences in weaning weights of calves out of Hereford-Charolais and Angus-Charolais cross cows. Parker et al. (1972) compared the maternal contribution to the weaning weight of calves produced by the mating of Angus bulls to Charolais, Hereford and F1 Charolais-Hereford cows in two locations. They found that the weaning weight of calves reared by F1 dams was 5 percent superior to the average for the straightbred cows at one of the locations.

Gregory et al. (1965) and Gaines et al. (1966) both reported greater heterosis for Hereford-sired calves from the mating of Hereford and Angus sires to Shorthorn dams. Pahnish et al. (1969) failed to show any differences between these same sire breeds when producing calves from Charolais cows. Tucker (1985) evaluated heterosis for preweaning traits using the same data that will be employed in this study. He observed that among the two-breed rotation crosses, Angus- and Hereford-sired calves from the first and third generations had larger estimates of heterosis for weaning weight than Charolais-sired calves. Heterosis estimates for the three- and four-breed rotations tended to be lower for the Charolais-sired calves than for the Angus- and Hereford-sired calves. Roberson et al. (1986) reported that Hereford-sired calves were heaviest at weaning for both Brahman and F1 dams, with backcross calves from F1 dams having the largest weaning weights.

Genetic Effects on Weaning Weight

Direct and Maternal Additive Breed Effects. These effects have been summarized in table 5. Negative direct (-18.4 to -1.6 kg) and positive maternal (8.0 to 13.9 kg) additive genetic differences between Angus and Hereford breeds were found (Dillard et al., 1980; Vaamonde and Franke, 1984; Koch et al., 1985; Morris et al., 1986; Wyatt and Franke, 1986). Gregory et al. (1978b) found a significant difference for maternal (8.5 kg, $P<.05$) additive genetic effects between the Angus and Hereford breeds for 200-d weight. Alenda et al. (1980) and MacNeil et al. (1982) reported direct additive genetic differences of -4.4 and 6.8 kg, respectively, and maternal additive genetic difference of 4.6 and 6.7 kg, respectively, between Angus and Hereford breeds for weaning weight. Peacock et al. (1981) failed to find significant effects of direct and maternal additive components on weaning weight for the Angus breed. Neville et al. (1984) reported a negative direct (-5.5 kg, $P<.01$) and a positive maternal (4.7 kg, $P<.05$) additive genetic difference between the Angus and Polled Hereford cattle for weaning weight. The maternal additive effect of the Angus breed was less ($P<.01$) than that of Charolais and greater ($P<.01$) than that of Hereford (MacNeil et al., 1982). Other studies have documented the maternal advantage of Angus over that of the Hereford breed (Gregory et al., 1965, 1978b, 1979; Smith et al., 1976).

TABLE 5. DIRECT AND MATERNAL ADDITIVE GENETIC EFFECTS FOR WEANING WEIGHT

Source	Breed deviation	Additive direct (kg)	Additive maternal (kg)
Gregory et al., 1978b	A-H	5.0	8.5*
Alenda et al., 1980	A	-8.5**	-4.1
	H	-4.1	-8.7*
	C	12.6**	12.8**
Dillard et al., 1980	A-H	-1.6	9.8**
	C-H	20.1**	28.6**
Peacock et al., 1981	A	-3.0	-1.7
	B	-26.6**	7.8**
	C	29.6**	-6.1*
MacNeil et al., 1982	A	-12.2	.3
	H	-19.0	-6.4
	C	12.4	6.3
Neville et al., 1984	A-PH	-5.5**	4.7*
	SG-PH	21.1**	16.2**
Vaamonde & Franke, 1984	B-A	12.8**	-.2
	H-A	18.4**	-13.9
Koch et al., 1985	A-H	-5.4**	11.0**
Morris et al., 1986	A-H	-3.0*	12.0**
Roberson et al., 1986	B-H	-12.9**	13.1**
Wyatt & Franke, 1986	H-A	3.2**	-9.5**
	B-A	2.5	3.7**
	C-A	42.0**	4.1

*P<.05.
**P<.01.
A = Angus, B = Brahman, C = Charolais, H = Hereford, PH = Polled Hereford, and SG = Santa Gertrudis.

Vaamonde and Franke (1984) reported a larger direct additive genetic effect for Brahman than Angus (12.8 kg, $P<.01$), whereas Wyatt and Franke (1986) reported a larger maternal additive genetic effect for Brahman than Angus (3.7 kg, $P<.05$). Peacock et al. (1981) reported a large but negative direct (-23.6 kg) and a positive maternal (9.5 kg) additive genetic difference between Brahman and Angus breeds. Roberson et al. (1986) obtained highly significant negative direct (-12.9 kg) and positive maternal (13.1 kg) additive breed effects on weaning weight due to Brahman relative to the Hereford. Koger et al. (1975) reported nonsignificant Brahman-Shorthorn deviations for direct and maternal additive effects on weaning weight. Peacock et al. (1981) attributed the negative direct additive effects for Brahman calves to the slow growth rate of the straightbred Brahman calves coupled with the large heterosis value for the Brahman crosses.

A large, positive Charolais direct additive effect on weaning weight was reported by several researchers (Notter et al., 1978; Alenda et al., 1980; Dillard et al., 1980; Peacock et al., 1981; MacNeil et al., 1982; Wyatt and Franke, 1986). The Charolais maternal additive effect was, however, not significantly different from that of Angus (Wyatt and Franke, 1986), although Alenda et al. (1980) and Dillard et al. (1980) reported a 22 to 29 kg increase in weaning weight from the Charolais maternal additive effect relative to that of Hereford. Maternal additive effects on weaning weight as deviations from the Hereford and Angus mean were 3.7 kg (Notter et al., 1978) and 9.4 kg for the Charolais breed (MacNeil et al., 1982). Peacock et al. (1981) reported a large advantage of the Charolais over the Angus breed for direct additive breed effect on 205-day weight.

Notter et al. (1978) quantified breed milk yields. Their study gave support to the positive maternal influence on calf weaning weight by large size breeds. This suggests that maternal additive effects may probably be mediated largely through the milking ability of the dam breed. Gregory et al. (1978b) and Wyatt and Franke (1986) suggested the possible existence of a positive association between milking ability and maternal additive effects on weaning weight. A negative genetic correlation between direct and maternal effects for weaning weight was, however, evident in other studies with beef cattle breeds (Mangus and Brinks, 1971; Koch, 1972; Kress et al., 1979; Bailey, 1981; Cantet et al., 1984; Nelsen et al., 1984). Neville et al. (1984) observed a negative relationship between transmitted and maternal genetic effects of Angus and a positive relationship for Santa Gertrudis cattle for 205-d weight. Gregory et al. (1978b) reported many more instances of positive than of negative relationships between transmitted and maternal genetic effects within the breeds studied.

Direct and Maternal Heterosis Effects. A summary of heterotic effects reported in the scientific literature is presented in table 6. MacNeil et al. (1982) reported average direct (4.4 kg) and maternal (6.8 kg) heterosis influences for 205-d weight for crosses involving Continental and British breeds of beef cattle.

Most studies have reported small, positive direct heterosis for the Angus-Hereford breed combination (4.8 to 6.9 kg, P<.01) for weaning weight (Gregory et al., 1978b; Dillard et al., 1980; Vaamonde and Franke, 1984; Koch et al., 1985; Morris et al., 1986; Wyatt and Franke, 1986) compared to the -12.5 kg reported by Alenda et al. (1980). Vaamonde and Franke (1984), Koch et al. (1985), Morris et al. (1986) and Wyatt and Franke (1986) reported significant estimates of Angus-Hereford maternal heterosis effect (4.0 to 15.0 kg) for weaning weight. Alenda et al. (1980) reported a negative .9 kg and Knapp et al. (1980) reported a positive 3.8 (2.2 %) kg maternal heterosis effect of Angus-Hereford crosses for weaning weight. Koch et al. (1985) reported a 12.8 kg (P<.01) increase in weaning weight due to Angus-Hereford maternal heterosis effect unadjusted for epistatic effects. Morris et al. (1986) also reported a 13.0 kg (P<.01) increase in weaning weight due to Angus-Hereford maternal heterosis effect unadjusted for epistatic and birthdate effects. Neville et al. (1984) reported direct heterosis estimates (10.7 and 7.8 kg, P<.01, respectively)

TABLE 6. DIRECT AND MATERNAL HETEROSIS EFFECTS FOR WEANING WEIGHT

Source	Breed combinations	Direct heterosis (kg)	Maternal heterosis (kg)
Gregory et al., 1978b	AH	6.4**	
Alenda et al., 1980	AH	-12.5	-.9
	AC	10.3	15.2**
	CH	-2.2	5.2
Dillard et al., 1980	AH	6.9**	
	AC	3.7	
	CH	9.5*	
Knapp et al., 1980	AH		3.8
	AC		-4.8
	CH		3.1
Peacock et al., 1981	AB	21.2**	28.9**
	AC	1.4	16.5**
	BC	16.5**	18.7**
Neville et al., 1984	APH	10.7**	
	ASG	7.8**	
	PHSG	21.8**	
Vaamonde & Franke, 1984	AH	6.1**	8.2**
	AB	25.0**	19.2**
	BH	25.2**	28.2**
Koch et al., 1985+	AH	6.9**	12.8**
Morris et al., 1986+	AH	6.0**	15.0**
Roberson et al., 1986	BH	21.6**	19.8**
Wyatt & Franke, 1986	AH	4.8**	4.0**
	AB	24.2**	13.0**
	AC	-.9	1.4
	BH	23.7**	17.7**
	BC	18.9**	
	CH	.8	7.5**

*P<.05.
**P<.01.
A = Angus, B = Brahman, C = Charolais, H = Hereford, PH = Polled Hereford, and SG = Santa Gertrudis.
+Heterosis effects were adjusted for additive * additive epistatic effects.

in Angus-Polled Hereford and Angus-Santa Gertrudis crosses for weaning weight.

Wyatt and Franke (1986) reported similar estimates of direct heterosis effects on weaning weight for Brahman-Angus and Brahman-Hereford (24.2 vs 23.7 kg). These results generally agree with the direct heterosis effects of 21.2 kg for Brahman-Angus (Peacock et al., 1981) and 21.6 kg (P<.01) for Brahman-Hereford (Roberson et al., 1986). Vaamonde and Franke (1984) also reported similar estimates (25.2 vs 25.0 kg) of direct heterosis effects on weaning weight for Brahman-Hereford and Brahman-Angus breed combinations. Peacock et al. (1981) and Wyatt and Franke (1986) reported similar estimates (16.5 vs 18.9 kg, P<.01) of Brahman-Charolais direct heterosis effects for weaning weight.

Estimates of maternal heterosis effects for weaning weight due to Brahman-Angus and Brahman-Hereford crosses were 13.0 and 17.7 kg (Wyatt and Franke, 1986; P<.01), respectively. Larger estimates of Angus-Brahman maternal heterosis effects for weaning weight, ranging from 19.2 to 28.9 kg, were reported in the scientific literature (McDonald and Turner, 1972; Peacock et al., 1981; Vaamonde and Franke, 1984). Similar maternal heterosis effects for the Brahman-Hereford cross, ranging from 19.8 to 28.8 kg (P<.01), were obtained by McDonald and Turner (1972), Vaamonde and Franke (1984) and Roberson et al. (1986).

Peacock et al. (1981) reported a Brahman-Charolais maternal heterosis effect of 18.7 kg (P<.01) for weaning weight.

Alenda et al. (1980) reported a 6.5 kg increase in 205 day weight due to the Charolais-Angus direct heterosis effect, whereas Dillard et al. (1980), Peacock et al. (1981) and Wyatt and Franke (1986) failed to show a significant direct heterosis response in crosses involving Angus and Charolais breeds (-.9 to 3.7 kg). Dillard et al. (1980) observed a 9.5 kg (P<.05) direct heterosis influence of Charolais-Hereford for weaning weight, compared to the -2.2 to .8 kg reported by Alenda et al. (1980) and Wyatt and Franke (1986).

Alenda et al. (1980) and Peacock et al. (1981) reported significant 15.2 to 16.5 kg increases in weaning weight due to Charolais-Angus maternal heterosis, compared to the -4.8 to 1.4 kg reported by Knapp et al. (1980) and Wyatt and Franke (1986). The 7.5 kg (P<.01) CH maternal heterosis effects for weaning weight reported by Wyatt and Franke (1986) was greater than the 3.1 to 5.2 kg estimates reported by Alenda et al. (1980) and Knapp et al. (1980).

<u>Condition Score at Weaning</u>

Condition score, also variously designated as weaning score, weaning grade, or slaughter grade at weaning, is a measure of fat cover on the calf at weaning. It is a function of the milk production level of the cow, the genetic expression of the calf for fattening and the environment in which the calf is raised (Vesely and Robison, 1971). Similarity between condition score and weaning weight was implied in the observations that calves growing fastest tended to also grade highest (McDonald, 1972; Sagebiel et al., 1974; Crockett et al., 1978; Gaines et al., 1978).

Condition score is also a reflection of some degree of thriftiness and adaptability of the individual calf as well as the maternal ability of the calf's dam under unfavorable environmental conditions. Crockett et al. (1978) and Peacock et al. (1978) observed that condition score was generally positively associated with live animal prices at weaning.

Heterosis for Condition Score. Hybrid vigor (heterosis) was found to significantly influence condition score (Gregory et al., 1965; Koger et al., 1975). Weaning condition score is apparently the calf trait with the widest range of heterosis values. Low negative estimates have been reported (Gaines et al., 1966; Humes et al., 1973) for crosses among the British breeds and Hereford inbred lines, respectively. Chapman et al. (1970) reported zero values from a study involving crossbred and grade calves with Angus, Polled Hereford and Santa Gertrudis breeding. A positive range of .10 to .30 units was reported by Gregory et al. (1965), Brinks et al. (1972), Long (1973), Long and Gregory (1974), Drewry et al. (1978), Gray et al. (1978) and Peacock et al. (1978) for inbred and outbred beef cattle crosses. Brinks et al. (1967) and Cundiff et al. (1974)

reported somewhat larger heterosis values of 2.6 to 4.5 percent for weaning score for crosses among Hereford inbred lines and the British breeds, respectively. Overall percentage heterosis for weaning score ranged from .0 to 1.8 percent (Gregory et al., 1965; Gaines et al., 1966; Sagebiel et al., 1967; Pahnish et al., 1969; Long, 1973; Long and Gregory, 1974; Gray et al., 1978). Turner and McDonald (1969) found no significant difference between crossbred and straightbred calves for condition score except for Brahman-Brangus crosses. Crockett et al. (1978) reported 9, 5 and 10 percent, respectively, heterosis levels for condition score for generations one to three in a rotational crossbreeding study.

McDonald (1972) found that singlecrosses averaged 4.4 % more for condition score than the parental mean. Angus-Brangus and Angus-Hereford crosses showed nonsignificant heterotic responses to condition score. Heterosis estimates for Angus-Hereford crosses ranged from -.10 to .24 units for weaning score (Gregory et al., 1965; Gaines et al., 1966; Rollins et al., 1969). Percentage heterosis for condition score generated from the crossing of Angus and Hereford breeds ranged from -1.7 to 3.0 % (Gregory et al., 1965; Gaines et al., 1966; Long and Gregory, 1974; Sagebiel et al., 1974; Crockett et al., 1978).

Heterosis estimates for weaning condition score due to Brahman-Angus crosses varied from .8 to 1.3 units (Damon et al.,1961; Peacock et al., 1978; Reynolds et al., 1982). Crockett et al. (1978) reported that Brahman crosses presented a 10.5 percent (P<.01) heterosis estimate for condition score when averaged over generations. Heterosis estimates for weaning score due to Angus-Brahman and Brahman-Hereford crosses were 11.0 and 10 %, respectively. Peacock et al. (1978) reported a significant difference of .40 units in weaning score between Angus-Brahman and Brahman-Angus calves. This is indicative of the importance of Brahman maternal additive genetic effect for condition score. Significant heterosis values of 5.5 and 9.8 percent, respectively, were obtained for Brahman-Charolais and Angus-Brahman calves for condition score at weaning. Reynolds et al. (1982) obtained an heterosis percentage of 16.7 (P<.01) from the average performance of Brahman-Angus and reciprocal cross calves. Franke (1980) reported a weighted heterosis estimate of .60 units in Brahman crosses for weaning score. Brahman-sired crossbred calves scored .30 units more than the straightbreds at weaning. Damon et al. (1961) obtained an heterosis estimate of .40 units for weaning score from Brahman-Hereford crosses.

Pahnish et al. (1969) reported that Angus-Charolais calves scored (4.3 vs 2.1 %) more than the Charolais-Angus crosses at weaning. Peacock et al. (1978) also found that Angus-Charolais calves scored (10.0 vs 9.7 units) more than Charolais-Angus calves at weaning. These results tend to suggest the influence of Charolais maternal effects for condition score. A heterosis level of 5.3 % ($P<.01$) for weaning score due to Angus-Charolais crosses was evident in this study. Angus-Charolais cross calves did not differ significantly from Brahman-sired crossbred calves in weaning score. The Brahman-Charolais heterosis estimate for weaning score was .50 units (Peacock et al., 1978).

McDonald (1972) observed that F1 dams, except those nursing Brahman-sired calves, having significant maternal heterosis for weaning weight generally expressed significant effects on condition of calf at weaning. This was attributed to the positive correlation ($r = .48$) between these two traits. The Brahman-sired calves lacked the growth potential to fully challenge their crossbred dams although they manifested the ability to fatten. It was concluded also that this response of Brahman-sired calves was indicative of their adaptation to the more favorable environmental conditions provided by their crossbred dams. McDonald (1972) also reported an estimate of cow heterosis averaged over all crosses for condition score of 5.4 percent.

Koger et al. (1975) reported heterosis values for condition score of 9.0 percent due to F1 calves out of straightbred dams compared with 14 % due to backcross calves from F1 dams, 8.0 % due to 5/8 Brahman-3/8 Shorthorn and reciprocal cross calves out of backcross dams and 5.0 % due to 7/8 Shorthorn-1/8 Brahman and reciprocal cross calves from backcross dams. Knapp et al. (1980) found that the Angus-Charolais cows gave a negative .50 % heterosis value while the Hereford-Angus cows gave a positive .80 % heterosis estimate for condition score. Knapp et al. (1980) and Koger et al. (1975) reported estimates of heterosis effects for the calf and maternal components combined of 1.7 and 17 %, respectively, for condition score.

Genetic Effects on Condition Score

Direct and Maternal Additive Breed Effects. These effects have been summarized in table 7. Dillard et al. (1980) reported that the direct and maternal additive genetic differences in weaning score between Angus and Hereford breeds were .29 ($P<.05$) and .20 grade points, respectively, in favor of the Angus. Peacock et al. (1981) found nonsignificant direct and maternal additive effects of Angus on weaning score of .13 and -.11 units, respectively. Neville et al. (1984) found a significant maternal additive effect of the Angus over the Polled Hereford of .40 units for weaning score. Olson et al. (1985) found highly significant differences in direct (2.05 units) and maternal (-.67 units) additive genetic effects for the Angus-Brown Swiss for condition score.

Koger et al. (1975) found large but nonsignificant direct and maternal breed additive effects of the Brahman over the Shorthorn breed for condition score. Peacock et al. (1981) obtained estimates of direct and maternal additive

TABLE 7. DIRECT AND MATERNAL ADDITIVE GENETIC EFFECTS FOR CONDITION SCORE

Source	Breed deviation	Additive direct (units)	Additive maternal (units)
Koger et al., 1975	B-S	.72	.74
Dillard et al., 1980	A-H	.29*	.20
	C-H	.31	.95**
Peacock et al., 1981	A	.13	-.11
	B	-.22*	.09
	C	.09	.01
Neville et al., 1984	A-PH	.00	.4**
	SG-PH	-1.3**	.7**
Olson et al., 1985	A-BS	2.05**	-.67**

*P<.05.
**P<.01.
A = Angus, B = Brahman, C = Charolais, BS = Brown Swiss, H = Hereford, S = Shorthorn, PH = Polled Hereford, and SG = Santa Gertrudis.

breed effects on weaning score of -.22 ($P<.05$) and .09 units, respectively, for the Brahman breed. Although the type of constraint employed in this study was not explained, it may be inferred that the breed additive genetic effects were estimated as deviations from zero.

Dillard et al. (1980) estimated direct and maternal additive genetic differences of .31 and .95 ($P<.01$) units, respectively, between the Charolais and Hereford breeds for condition score. It was evident from this study that the Charolais maternal ability exceeded that of Hereford and Angus and accounted for significant amounts of variation in type score. However, Peacock et al. (1981) found no significant effects of Charolais direct and maternal additive genetic components on weaning score. Large but negative direct (-1.3 units, $P<.01$) and small maternal (.70 units, $P<.01$) additive genetic differences between Santa Gertrudis and Polled Hereford were reported for condition score at weaning (Neville et al., 1984).

Direct and Maternal Heterosis Effects. These effects adapted from different sources are presented in table 8. Estimates of Angus-Hereford direct (.15 units) and maternal (.60 units) heterosis effects for condition score were reported by Dillard et al. (1980) and Knapp et al. (1980), respectively. Peacock et al. (1981) reported that estimates of Angus-Brahman direct and maternal heterosis effects for condition score were 1.00 and .94 units (P<.01), respectively.

Dillard et al. (1980) and Peacock et al. (1981) reported that estimates of the Angus-Charolais direct heterosis effect for condition score was .43 and .33 (P<.01) units, respectively. Peacock et al. (1981) obtained an estimate of the Angus-Charolais maternal heterosis effect for condition score of .41 units (P<.01) compared to the -.40 units reported by Knapp et al. (1980). Neville et al. (1984) reported a small direct heterosis effect for Angus-Polled Hereford (.10 units) and a significant direct heterosis effect for Polled Hereford-Santa Gertrudis crosses for weaning score.

Estimates of direct and maternal heterosis effects of Brahman-Shorthorn crosses for weaning score were .70 (8.1 %) and .81 (9.4 %) units, respectively (Koger et al., 1975). Peacock et al. (1981) found highly significant direct and maternal heterosis effects of Brahman-Charolais crosses on weaning score of .43 and .47 units, respectively. Dillard et al. (1980) found a direct Hereford-Charolais heterosis effect on weaning score of .49 (P<.05). Knapp et al. (1980) found a zero estimate of Hereford-Charolais maternal heterosis effect on condition score. However, Neville et al. (1984) reported a direct heterosis effect averaged over all generations of a rotational crossbreeding study of .50 units (P<.01) in Polled Hereford-Santa Gertrudis crosses for

TABLE 8. DIRECT AND MATERNAL HETEROSIS EFFECTS FOR CONDITION SCORE

Source	Breed combinations	Direct heterosis (units)	Maternal heterosis (units)
Dillard et al., 1980	AH	.15	
	AC	.43	
	CH	.49*	
Knapp et al., 1980	AH		.6
	AC		-.4
	CH		.0
Peacock et al., 1981	AB	1.0**	.94**
	AC	.33**	.41**
	BC	.43**	.47**
Neville et al., 1984	APH	.1	
	ASG	.0	
	PHSG	.5**	

*P<.05.
**P<.01.
A = Angus, B = Brahman, C = Charolais, H = Hereford, PH = Polled Hereford, and SG = Santa Gertrudis.

condition score. These results tend to confirm the presence of considerable variation in heterosis effects for condition score.

Conclusion

Heterosis may be defined as the deviation of the average of reciprocal crossbred progeny from that of the straightbred parent breeds for any given trait and under a specified set of conditions. Individual heterosis refers to the amount of hybrid vigor attributable to the increased heterozygosity of the outbred individual as manifested in each preweaning trait. This increase will be favorable if the dominance effect at most of the contributing loci improves preweaning performance (Sellier, 1976). Maternal heterosis is the hybrid advantage due to increased heterozygosity in the crossbred dam of the individuals being measured over and above that in their straightbred contemporaries. This is reflected in better maternal behavior and (or) increased milk production of the crossbred females relative to the straightbreds. In other words, many traits are influenced not only by the genotype of the offspring but also by the maternal environment provided by the dam.

Preweaning growth traits in beef cattle are affected also by the size of the dam. Miquel et al. (1972) found that large cows with increased nutrient requirements usually compensate by producing large progeny. Weaning weight is influenced by the amount of milk produced by the dam. Heterosis for any trait also depends on the breeds making up the cross since, theoretically, it is a function of the gene frequency differences and level of dominance at loci affecting the trait (Falconer, 1982).

This review also suggests that realized heterosis may be dependent upon the environment in which the experiments were conducted. This reflects the possible presence of genotype by environment interactions for these heterotic effects. Barlow (1981) and Hohenboken (1985) noted that the amount of heterosis from breed crossing could vary with the environmental circumstances to which the population was subjected. Young (1971), working with Drosophila, found that hybrid vigor was least under optimum conditions and greatest under less desirable conditions for growth. Heterosis effects were different within and among the preweaning traits for the different studies reported.

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CHAPTER II

DIRECT AND MATERNAL ADDITIVE AND HETEROTIC GENETIC EFFECTS ON PREWEANING TRAITS IN BEEF CATTLE

Summary

A total of 2,945 calf records from the Ben Hur Crossbreeding Unit of the Louisiana Agricultural Experiment Station, Baton Rouge, were available for this study. These data were collected during four periods, designated as generations 1, 2, 3 and 4, of a long-term rotational crossbreeding experiment. Each generation contained Angus (A), Brahman (B), Charolais (C) and Hereford (H) straightbreds, A-B, C-B, and H-B two-breed, A-H-B, C-A-B and C-H-B three-breed and A-B-C-H four-breed rotational combinations. Each of the rotational breed combinations differed in proportion of breed inheritance from generation to generation. Estimates of direct and maternal additive (Ig and Mg) and heterotic (Ih and Mh) genetic effects were determined using a regression approach. Birth weight (BWT), preweaning daily gain (ADG), weaning weight (WWT) and condition score (SCORE) were examined. The regression model contained, in addition to the genetic effects, an overall mean, generation and year subclass, sex of calf, covariates (calf weaning age (or Julian birthdate in the case of BWT) and age of dam) and a residual term. Direct and maternal additive and heterotic genetic effects were computed as

deviations from the overall mean for each preweaning trait. Effects of IgA and IgB on ADG, WWT and SCORE were negative. The IgC effect was positive for all traits while the IgH effect was positive for ADG and SCORE. The MgA effect was greatest for BWT while the MgC effect exceeded all other breeds for WWT. The MgB effect was lowest for BWT but largest for ADG and SCORE while the MgH effect was lowest for all traits except BWT. The AB, AC, AH, BC, BH, and CH direct heterosis effects were important for all traits except SCORE to which only AB and BH contributed significantly. Brahman crosses had the greatest amount of direct heterosis influence on all preweaning traits. Hereford crosses manifested significant maternal heterosis effects on ADG, WWT and SCORE.

(Key Words: Crossbreeding, Direct Additive, Maternal Additive, Direct Heterosis, Maternal Heterosis).

Introduction

Estimating genetic parameters such as direct (Ig) and maternal (Mg) additive genetic effects of breeds (or lines) and direct (Ih) and maternal (Mh) heterotic genetic effects of breed combinations is of utmost importance in animal genetics. These parameters are useful for purposes of prediction and decision-making relative to the design and application of effective and efficient breeding experiments and to the maximization of production efficiency. Methods of deriving the potential contributions of each breed to genetic effects in any crossbreeding system were defined in terms of genetic expectations by Dickerson (1969, 1973). McDonald and Turner (1972), Gregory et al. (1978b) and Alenda et al. (1980) contrasted least-squares breed group means while Koger et al. (1975), Dillard et al. (1980) and Robison et al. (1981) utilized the regression approach to obtain estimates of some genetic effects.

The regression technique has since been applied to the evaluation of genetic effects for preweaning traits of different combinations of beef and dairy breeds under varying environmental conditions (MacNeil et al., 1982; Vaamonde and Franke, 1984; Roberson et al., 1986; Wyatt and Franke, 1986). Estimates of additive and heterotic genetic effects have been reported by various researchers for different combinations of the Angus, Brahman, Charolais and Hereford breeds but never for all four breeds under the same conditions. Also the results could be applicable only to conditions similar to those under which the experiments were conducted (Barlow, 1981).

The objectives of this study were to estimate the additive direct and maternal genetic effects of Angus, Brahman, Charolais and Hereford breeds, and to determine the direct and maternal heterosis effects of these breed combinations.

Materials and Methods

Source of Data. Preweaning growth data for the straightbred and crossbred beef cattle were collected from the Ben Hur Beef Cattle Crossbreeding Unit of the Louisiana Agricultural Experiment Station during the period from 1970 to 1986. These data were generated by 4 straightbred lines including Angus (A), Brahman (B), Charolais (C) and Hereford (H) and 7 rotational crossbred lines involving two-breed (A-B, C-B, H-B), three-breed (A-H-B, C-A-B, C-H-B) and four-breed (A-B-C-H) rotational combinations.

Data consisted of complete records from generations 1, 2 and 3 and a portion of generation 4. Each generation was designed to last for 5 yr and generations were non-overlapping. Records included calf crop year, calf's age at weaning (WA) in days, Julian birthdate (BD) in days, calf breedtype, dam breedtype, dam age at weaning (CA) in years, birth weight (BWT), preweaning average daily gain (ADG = (WWT - BWT) / WA), weaning weight (WWT) and condition score (SCORE). Condition score is a subjective evaluation of the fat covering on a calf at weaning. It was assigned by a panel on the basis of USDA quality scores with 11 = high good, 12 = low choice, 13 = average choice, etc., and recorded as an average score for each animal. The expected breed composition of each calf breedtype and the number of calves produced are presented in table 9.

Management of Cattle. Breeding females were randomly assigned according to their breed type and age to breeding herds each mating season. Twenty-five to 30 females were maintained in each herd with a single bull. Bulls were weighed, dewormed and semen tested prior to being placed within the breeding herds for a 75 day breeding season, with pasture matings beginning April 15 of each year. Bulls were purchased from Louisiana breeders and chosen on the basis of structural soundness, size and fertility of their dams. Bulls were used first at 2 yr of age and for only two breeding seasons in order to sample as many bulls as possible.

Cows were wintered on native hay, fortified blackstrap molasses and overseeded ryegrass. Although the feedstuffs for the wintering program probably varied from year to year, the rations were assumed to meet NRC requirements. Breeding herds were grazed on common bermudagrass and dallisgrass pastures during the summer. Persian and Louisiana S-1 white clover were available during the early spring.

Cows that failed to produce a calf in two consecutive years, or that presented some structural unsoundness that could impair their productivity, or that had some reproductive abnormalities, were culled from the herd. However, no deliberate selection for any of the production

TABLE 9. BREED COMBINATIONS, EXPECTED BREED COMPOSITION AND FREQUENCY DISTRIBUTION BY GENERATION

Mating type and breed combinations	Generation			
	1	2	3	4
<u>Straightbreds</u>				
Angus (A)	A (96)	A (71)	A (81)	A (22)
Brahman (B)	B (66)	B (58)	B (47)	B (20)
Charolais (C)	C (87)	C (64)	C (76)	C (19)
Hereford (H)	H (68)	H (63)	H (93)	H (22)
<u>Two-breed rotations</u>[a]				
A-B	A3B1 (81)	B5A3 (72)	A11B5 (78)	B21A11 (23)
C-B	C3B1 (87)	B5C3 (69)	C11B5 (85)	B21C11 (25)
H-B	H3B1 (95)	B5H3 (82)	H11B5 (113)	B21H11 (21)
<u>Three-breed rotations</u>[a]				
A-B-C	C2A1B1 (76)	A5C2B1 (91)	B9A5C2 (93)	C18B9A5 (23)
A-B-H	A2H1B1 (112)	H5A2B1 (92)	B9H5A2 (89)	A18B9H5 (27)
B-C-H	C2H1B1 (82)	H5C2B1 (94)	B9H5C2 (87)	C18B9H5 (24)
<u>Four-breed rotation</u>[a]				
A-B-C-H	H2A1B1(84)	C4H2A1B1(71)	B9C4H2A1(92)	A17B9C4H5(24)

[a]Figures within breed groups represent proportion of breeding of specific breeds in the crossbred individual. For example, A3B1 designates 3/4 Angus and 1/4 Brahman breeding in this crossbred progeny.
Numbers in parentheses represent number of calves for each breeding group.

traits was applied to any female involved in this study. Calves were generally born between January 15 and April 1 of each year and were weaned the first week in October at an average age of 220 days. All calves were weighed, dehorned and identified at birth. Male progeny were castrated at 5 months of age and maintained with the heifer calves until weaning. At weaning all calves were treated against various calfhood diseases. Heifer calves were grown out on pasture and managed to gain approximately .57 kg a day before being exposed for breeding as yearlings. These yearling heifers were bred to small size breeds of bulls that were unrelated to breeds included in this study and calved first at 2 yr of age. The goal was to allow for the comparison of maternal performance of these yearling heifers before their incorporation into the next generation of the project. However, the last calf crop of each generation was exposed for breeding only to rotation bulls. All heifer calves weighed, on the average, about 275 kg at the time of first exposure to the sires of unrelated breeds.

Rotational Crossbreeding Systems. A rotational crossbreeding scheme may encompass two or more breeds of livestock. A comprehensive review of rotational systems was presented by Hohenboken (1985) and Chapman and Franke (1987). The primary advantage of the rotational mating system over other crossbreeding systems lies in the retention of crossbred females as herd replacements.

Estimation Methodology. The first attempt to estimate different kinds of gene action involved in single-cross yield heterosis was provided by Sprague and Tatum (1942). These effects were separated into two classes called general and specific combining abilities. Differences in general combining ability primarily involve additive genetic effects while the specific combining ability include nonadditive genetic effects. General combining ability (gca) can be expressed as a function of the breed of origin (sire and dam) of the two haploid sets of genes that make up the cross (Gaines et al., 1970).

Henderson (1952) reported that the expected performance of a cross was a function of the general combining abilities of the lines (or breeds) involved in the cross and the maternal abilities of the female lines producing the cross. The distinction among the offspring of each cross is based on the relative magnitude of the genetic material (or germplasm) contributed by each breed or line. Various interpretations have been given to the genetic effects derived from different mating systems (Trail et al., 1982; Eisen et al., 1983; Newman et al., 1986).

Dickerson (1969, 1973) presented information that is useful in deriving the joint effects of breed complementation and heterozygosity in specific outcrossing systems. These methods involve the development of mathematical models that describe the contributions to the phenotypic average of a given trait among the straightbred or crossbred groups of cattle. These models are generally composed of direct, maternal and grandmaternal additive (Ig, Mg, Mg'), heterotic (Ih, Mh Mh') and gametic recombination (Ir, Mr, Mr') effects, respectively, for a given cross. These components were defined as mean deviations in progeny performance from the average performance of the straightbreds of a specified set of breeds. Establishment of these equations was based on the assumption that the phenotype is a linear function of the direct and maternal effects and that the association between phenotype and degree of heterozygosity in the cross is linear.

Statistical Methodology. Dickerson's models are useful in comparing different outbreeding systems for their ability to utilize breed complementation and direct and maternal heterosis effects. These methods have been employed to compare crossbreeding systems in sheep (Nitter, 1978), swine (Sellier, 1976) and beef cattle (Damon et al., 1961; Gregory et al., 1978b; Alenda et al., 1980). Estimates of the average genetic and heterosis effects can simultaneously be obtained using the linear regression method after suitable mathematical constraints have been imposed. This approach has been used to estimate genetic effects for dairy production traits (Robison et al., 1981) and for beef production traits (Dillard et al., 1980; Wyatt and Franke, 1986). The statistical theory of this approach was reviewed by Fimland (1983).

Robison et al. (1981) reported that the regression procedure (Dillard et al., 1980) provided results identical to those derived by estimating least-squares breed group means, equating them to their corresponding genetic expectations (Dickerson, 1969, 1973; Alenda et al., 1980), weighting each mean by the number of observations and solving the system of equations (least-squares-means-constrast method). Using a data set simulated with known values of the genetic effects, they were able to recover the appropriate values, thereby validating the regression approach.

Alenda et al. (1980) suggested that estimates of direct and maternal additive genetic effects were biased by the presence of within-breed dominance and epistatic effects. These genetic effects have generally been assumed to be negligible. Sprague (1983) suggested also that effects associated with epistasis or genotype by environment interactions were likely to introduce significant biases in hybrid predictions. He noted, however, that the effects due to the genotype by environment interactions were apparently more important than those due to epistasis.

The statistical (or regression) model used to estimate the genetic parameters was based on the following definitions and assumptions:

1) The presence of a linear association between heterosis

and breed heterozygosity.

2) All genetic factors, namely, direct and maternal additive genetic effects and direct and maternal heterosis effects, were considered as fixed effects.

3) Overparameterization of the genetic model necessitated linear restrictions (IgA + IgB + IgC + IgH = MgA + MgB + MgC + MgH = 0) so as to reduce the number of equations to equal the number of degrees of freedom.

4) Measures of the proportion of genes contributed by the respective breeds (A, B, C or H) and measures of the level of heterozygosity due to the respective breed combinations (AB, AC, AH, BC, BH or CH) in the cross were assumed to be continuous independent variables. These measures (weighting factors) were derived based on the assumption of independent loci with each locus made up of two alleles. The expected level of heterozygosity was measured on a scale of zero (minimum value) for the average heterozygosity in the parental breeds to one (maximum value) for the average heterozygosity in their F1 progeny. These weighting factors were calculated for each breeding structure. Matrices of breed proportions and degree of heterozygosity in the progeny of the different mating types are presented in tables 10a and 10b.

5) Alenda et al. (1980) and Dillard et al. (1980) defined additive effects for Igi and Mgi to contain, in addition to the additive genetic effects of breed i, the within-breed

TABLE 10a. DESIGN MATRIX OF MULTIPLIERS FOR THE ESTIMATION OF DIRECT ADDITIVE AND HETEROTIC EFFECTS FOR PREWEANING TRAITS[1]

Mating type[2]	Direct additive				Direct heterotic					
Sire*Dam	A	B	C	H	AB	AC	AH	BC	BH	CH
A*A	1	0	0	0	0	0	0	0	0	0
B*B	0	1	0	0	0	0	0	0	0	0
C*C	0	0	1	0	0	0	0	0	0	0
H*H	0	0	0	1	0	0	0	0	0	0
A*A1B1	3/4	1/4	0	0	1/2	0	0	0	0	0
C*C1B1	0	1/4	3/4	0	0	0	0	1/2	0	0
H*H1B1	0	1/4	0	3/4	0	0	0	0	1/2	0
C*A1B1	1/4	1/4	1/2	0	0	1/2	0	1/2	0	0
A*H1B1	1/2	1/4	0	1/4	1/2	0	1/2	0	0	0
C*H1B1	0	1/4	1/2	1/4	0	0	0	1/2	0	1/2
H*A1B1	1/4	1/4	0	1/2	0	0	1/2	0	1/2	0
B*A3B1	3/8	5/8	0	0	3/4	0	0	0	0	0
B*C3B1	0	5/8	3/8	0	0	0	0	3/4	0	0
B*H3B1	0	5/8	0	3/8	0	0	0	0	3/4	0
A*C2A1B1	5/8	1/8	1/4	0	1/4	1/2	0	0	0	0
H*A2H1B1	1/4	1/8	0	5/8	0	0	1/2	0	1/4	0
H*C2H1B1	0	1/8	1/4	5/8	0	0	0	0	1/4	1/2
C*H2A1B1	1/8	1/8	1/2	1/4	0	1/4	0	1/4	0	1/2
A*B5A3	11/16	5/16	0	0	5/8	0	0	0	0	0
C*B5C3	0	5/16	11/16	0	0	0	0	5/8	0	0
H*B5H3	0	5/16	0	11/16	0	0	0	0	5/8	0
B*A5C2B1	5/16	9/16	1/8	0	5/8	0	0	1/4	0	0
B*H5A2B1	1/8	9/16	0	5/16	1/4	0	0	0	5/8	0
B*H5C2B1	0	9/16	1/8	5/16	0	0	0	1/4	5/8	0
B*C4H2A1B1	1/16	9/16	1/4	1/8	1/8	0	0	1/2	1/4	0
B*A11B5	11/32	21/32	0	0	11/16	0	0	0	0	0
B*C11B5	0	21/32	11/32	0	0	0	0	11/16	0	0
B*H11B5	0	21/32	0	11/32	0	0	0	0	11/16	0
C*B9A5C2	5/32	9/32	18/32	0	0	5/16	0	9/16	0	0
A*B9H5A2	18/32	9/32	0	5/32	9/16	0	5/16	0	0	0
C*B9H5C2	0	9/32	18/32	5/32	0	0	0	9/16	0	5/16
A*B9C4H2A1	17/32	9/32	4/32	2/32	9/16	1/4	1/8	0	0	0

[1]Igi = Individual (direct) additive breed effect for the ith breed in the progeny, and
Ihij = Individual heterotic effect for the ijth breed combination in the crossbred progeny.

[2]A = Angus, B = Brahman, C = Charolais and H = Hereford.

TABLE 10b. DESIGN MATRIX OF MULTIPLIERS FOR THE ESTIMATION OF MATERNAL ADDITIVE AND HETEROTIC EFFECTS FOR PREWEANING TRAITS[1]

Mating type[2]	Maternal additive				Maternal heterotic					
Sire*Dam	A	B	C	H	AB	AC	AH	BC	BH	CH
A*A	1	0	0	0	0	0	0	0	0	0
B*B	0	1	0	0	0	0	0	0	0	0
C*C	0	0	1	0	0	0	0	0	0	0
H*H	0	0	0	1	0	0	0	0	0	0
A*A1B1	1/2	1/2	0	0	1	0	0	0	0	0
C*C1B1	0	1/2	1/2	0	0	0	0	1	0	0
H*H1B1	0	1/2	0	1/2	0	0	0	0	1	0
C*A1B1	1/2	1/2	0	0	1	0	0	0	0	0
A*H1B1	0	1/2	0	1/2	0	0	0	0	1	0
C*H1B1	0	1/2	0	1/2	0	0	0	0	1	0
H*A1B1	1/2	1/2	0	0	1	0	0	0	0	0
B*A3B1	3/4	1/4	0	0	1/2	0	0	0	0	0
B*C3B1	0	1/4	3/4	0	0	0	0	1/2	0	0
B*H3B1	0	1/4	0	3/4	0	0	0	0	1/2	0
A*C2A1B1	1/4	1/4	1/2	0	0	1/2	0	1/2	0	0
H*A2H1B1	1/2	1/4	0	1/4	1/2	0	1/2	0	0	0
H*C2H1B1	0	1/4	1/2	1/4	0	0	0	1/2	0	1/2
C*H2A1B1	1/4	1/4	0	1/2	0	0	1/2	0	1/2	0
A*B5A3	3/8	5/8	0	0	3/4	0	0	0	0	0
C*B5C3	0	5/8	3/8	0	0	0	0	3/4	0	0
H*B5H3	0	5/8	0	3/8	0	0	0	0	3/4	0
B*A5C2B1	5/8	1/8	1/4	0	1/4	1/2	0	0	0	0
B*H5A2B1	1/4	1/8	0	5/8	0	0	1/2	0	1/4	0
B*H5C2B1	0	1/8	1/4	5/8	0	0	0	0	1/4	1/2
B*C4H2A1B1	1/8	1/8	1/2	1/4	0	1/4	0	1/4	0	1/2
B*A11B5	11/16	5/16	0	0	5/8	0	0	0	0	0
B*C11B5	0	5/16	11/16	0	0	0	0	5/8	0	0
B*H11B5	0	5/16	0	11/16	0	0	0	0	5/8	0
C*B9A5C2	5/16	9/16	1/8	0	5/8	0	0	1/4	0	0
A*B9H5A2	1/8	9/16	0	5/16	1/4	0	0	0	5/8	0
C*B9H5C2	0	9/16	1/8	5/16	0	0	0	1/4	5/8	0
A*B9C4H2A1	1/16	9/16	1/4	1/8	1/8	0	0	1/2	1/4	0

[1]Mgi = maternal (indirect) additive breed effect for the ith dam breed in the dam of the calf, and
Mhij = maternal heterotic effect for the ijth breed combination in the crossbred dam of the calf.
[2]A = Angus, B = Brahman, C = Charolais and H = Hereford.

dominance and epistatic effects. The additive effect (also called average genetic effect) was assumed to be the predominant source of variation.

6) Sex-linked and epistatic effects as well as grandmaternal additive and heterotic genetic effects were considered to be negligible.

7) Heterosis effect was defined as the deviation of the average heterozygosity of the parental breeds from that of the F1 crossbreds. Heterosis was considered as an aggregation of the product of the squared differences in gene frequency between breeds and the favorable dominance effects generated by the crossing of these breeds at the independent loci controlling a specific trait (Falconer, 1983). Heterosis effects (Ihij and Mhij) were defined to contain breed interaction effects due to both dominance and epistasis (Alenda et al., 1980; Dillard et al., 1980). However, the assumption was made that the major force shaping the responses was the dominance effect. Additive and dominance effects were assumed to be uncorrelated.

The regression model used to estimate the genetic parameters was developed as follows:

$$
\begin{aligned}
Y = mu &+ fA*IgA + fB*IgB + fC*IgC + fH*IgH \\
&+ fAB*IhAB + fAC*IhAC + fAH*IhAH \\
&+ fBC*IhBC + fBH*IhBH + fCH*IhCH \\
&+ f'A*MgA + f'B*MgB + f'C*MgC + f'H*MgH \\
&+ f'AB*MhAB + f'AC*MhAC + f'AH*MhAH
\end{aligned}
$$

$$+ f'BC*MhBC + f'BH*MhBH + f'CH*MhCH$$
$$+ gy + sex + b1\ (A - 227.5) + b2\ (D - 5.5)$$
$$+ c1\ (A - 227.5)^2 + c2\ (D - 5.5)^2 + error,$$

where,

Y = observed calf trait (BWT, ADG, WWT or SCORE),

mu = overall mean,

Ig and Mg = direct and maternal additive genetic effects, respectively, for the respective breeds (A, B, C or H),

Ih and Mh = direct and maternal heterosis genetic effects, respectively, for the respective breed combinations (AB, AC, AH, BC, BH or CH),

f and f' = proportion of genes in calf or dam from their respective sire and dam components, or proportion of loci with genes from one breed paired with genes from another breed in the calf or dam,

gy = generation-year subclass effect,

b1 and b2 = partial linear regression on calf age at weaning (or Julian birthdate in the case of BWT) in days and dam age at calf birth in years, respectively,

c1 and c2 = partial quadratic regression on calf weaning age (or Julian birthdate in case of BWT) and dam age, respectively,

error = assumed to be normally and independently distributed with mean of zero and variance = $\sigma 2$.

Least-squares procedures (SAS, 1982) were used to compute sources of variation and partial regression coefficients for the different genetic effects in the model. Because of linear dependencies, the coefficients of IgH and MgH effects were, respectively, subtracted from their corresponding counterparts before the analysis (Gallivan et al., 1987). Using the definition that estimates of IgA, IgB, IgC and IgH effects and their maternal components, respectively, are deviations from the mean and thus sum to zero, IgH and MgH effects were in turn estimated as follows:

$$IgH = - (IgA + IgB + IgC),$$

$$MgH = - (MgA + MgB + MgC).$$

Least-squares contrast procedures in SAS (1982) were used to calculate estimates of IgH and MgH effects and their standard errors using the linear functions above.

Results and Discussion

Least-squares analysis of variance mean squares and significance levels for each preweaning trait are presented in table 11. All extraneous sources of variation (non genetic effects) that accounted for significant reductions in the variation of these preweaning traits were included in the final model. Estimates of direct and maternal additive genetic effects and of direct and maternal heterosis effects for each preweaning trait were calculated as deviations from the overall least-squares mean. The partial regression coefficients for heterosis effects represent the average difference between crossbred and straightbred calves or dams for each preweaning trait.

Birth Weight. Birth weight is subject to the influence of differences in prenatal maternal environment among breeds or genotypes of dams. This is reflected in the significance of the maternal additive genetic effects for this trait. The IgA and IgC effects were also significant sources of variation for BWT, suggesting the importance of some breed additive effects for this trait.

Partial regression coefficients for the estimates of direct and maternal additive genetic effects for BWT are shown in table 12. The IgC and MgC effects for BWT were 5.2

TABLE 11. LEAST-SQUARES ANALYSIS OF VARIANCE MEAN SQUARES FOR CALF PREWEANING TRAITS

Sources of variation	df	Birth weight (kg^2)	Preweaning ADG $(kg/day)^2$	Weaning weight (kg^2)	Condition score $(units)^2$
gy[a]	13	203.6**	.274**	14522.4**	119.1**
sex	1	4120.2**	4.199**	280066.1**	165.1**
BD(WA)[b]	1	3738.7**	.044*	295422.2**	70.7**
BD*BD(WA*WA)	1	430.8**	.069**	6753.8**	3.4+
CA[c]	1	1163.9**	.479**	35968.0**	31.3**
CA*CA	1	1295.1**	.382**	31534.5**	17.0**
IgA	1	1130.8**	.073**	9576.0**	8.9**
IgB	1	5.0	.065**	2703.3*	11.2**
IgC	1	1424.6**	.285**	25895.1**	12.4**
IhAB	1	430.7**	.326**	22094.1**	12.2**
IhAC	1	55.3+	.040*	1547.9+	.2
IhAH	1	176.9**	.051**	4418.3**	.4
IhBC	1	539.2**	.203**	15074.2**	3.5+
IhBH	1	424.9**	.225**	16053.6**	9.5**
IhCH	1	125.8*	.067**	5580.5**	3.4+
MgA	1	201.3**	.013	198.8	.0
MgB	1	552.9**	.150**	4248.4**	10.3**
MgC	1	143.3**	.141**	9145.4**	8.1**
MhAB	1	82.6*	.002	6.0	.1
MhAC	1	28.1	.023+	1562.7+	.3
MhAH	1	17.3	.119**	6800.5**	14.8**
MhBC	1	262.2**	.000	225.2	.0
MhBH	1	63.7+	.079**	3067.8*	3.5+
MhCH	1	3.9	.066**	3590.2**	6.2*
Residual	2908	21.2	.009	515.2	1.2
R^2(%)		44.6	54.7	62.1	44.1
CV		14.1	11.0	10.2	9.9

[a]generation-year subclass effect.
[b]BD is Julian birthdate in days (used to adjust birth weight for effects due to season of birth),
WA is calf age at weaning in days (used to adjust all traits except birth weight for differences in weaning age).
[c]CA is age of dam at calving in years.
**P<.01.
*P<.05.
+P<.10.

TABLE 12. BREED DIRECT AND MATERNAL ADDITIVE EFFECTS FOR BIRTH WEIGHT (kg)

		Additive effects	
Breed	No. of observations	Direct b±SE[a]	Maternal b±SE
Angus	1,398	-4.2±.6**	1.8±.6**
Brahman	2,183	.4±.9	-4.2±.8**
Charolais	1,353	5.2±.6**	1.6±.6**
Hereford	1,435	-1.4±.6*	.8±.6

**P<.01.
*P<.05.
[a]Partial regression coefficient and standard error.

and 1.6 kg (P<.01), respectively. The IgC effect for BWT was 7 to 9 kg larger than those of A and H. Alenda et al. (1980), Dillard et al. (1980) and Wyatt and Franke (1986) found similar results for BWT for the IgC effect relative to H and A. The MgC effect for BWT was .2 kg less than that of Angus. This difference was, however, larger than the -3 to-2 kg reported by Alenda et al. (1980) and Wyatt and Franke (1986). The MgC effect for BWT was .8 kg more than that of Hereford, a difference that was smaller than the 2.5 kg reported by Dillard et al. (1980) but larger than the -3 kg reported by Alenda et al. (1980). These findings tend to suggest the importance of both the transmitting and maternal abilities of the Charolais breed relative to the *in utero* growth of their calf compared to those of the British and Brahman breeds.

The IgA effect decreased birth weight (-4.2 kg, P<.01) whereas the MgA component increased BWT by 1.8 kg (P<.01). Gaines et al. (1970) and Alenda et al. (1980) found similar but nonsignificant results in their studies. The IgA effect for BWT was 2.8 kg less than that of Hereford. These results are in general agreement with those of Koch et al. (1985), Morris et al. (1986) and Wyatt and Franke (1986) but differ from those of Gregory et al. (1978b), Dillard et al. (1980) and Vaamonde and Franke (1984). The MgA effect for BWT was 1.0 kg more than that of Hereford. Gregory et al. (1978b), Dillard et al. (1980) and Vaamonde and Franke (1984) reported similar results for BWT when the MgA effect was deviated from Hereford. In contrast, Koch et al. (1985), Morris et al. (1986) and Wyatt and Franke (1986) found low negative estimates for the MgA effect on BWT relative to the Hereford. These findings tend to support the contention that Angus dams generally demonstrate greater maternal support for the growth of their calves in utero than the Hereford dams.

The MgB effect for BWT was -4.2 kg (P<.01) while the IgB effect for BWT was .4 kg. The IgB effect for BWT ranged from 2 to 5 kg more than those of Angus and Hereford while the MgB effect ranged from 5 to 6 kg less than those of Angus and Hereford, respectively. Roberson et al. (1986) found similar results for BWT when IgB and MgB effects were deviated from Hereford. Vaamonde and Franke (1984) and Wyatt and Franke (1986) found larger estimates of the IgB effect for BWT relative to the Angus breed than the 4.6 kg reported in this study. However, they reported similar results for the MgB effect on BWT relative to the Angus breed. Comerford et al. (1987) reported a 4.2 kg larger IgB effect for BWT relative to the Hereford breed than the 1.8 kg found in this study. The MgB effect for BWT was 5.0 kg less than that of Hereford. This B-H maternal additive genetic difference was smaller than the -9.0 kg difference for B-H reported by Comerford et al. (1987). The sampling of Brahman sires under the different conditions of these studies could also have contributed to the observed variation.

The IgH effect tended to decrease (-1.4 kg, $P<.05$) birth weight while the MgH component increased BWT (.8 kg). Alenda et al. (1980) reported similar results for BWT relative to the IgH and MgH effects. Comerford et al. (1987), in a diallel analysis of birth weights of Brahman and Hereford breeds, also found that the IgH effect tended to decrease BWT while the MgH component had a tendency to increase BWT ($P<.05$). Gaines et al. (1970) reported 3.8 kg Ig(H-A) and -1.7 kg Mg(H-A) effects for BWT. However, in their study, the method of estimation was based on a diallel analysis involving Angus, Hereford and Shorthorn breeds and the estimates realized were associated with relatively large standard errors.

This study found that C had the largest direct genetic effect for BWT while A had the lowest, with the B and H breeds being intermediate. The C and A breeds manifested the largest maternal support for the *in utero* growth of their calves. The B breed had the least maternal influence on BWT while H was intermediate in maternal additive influence on BWT.

Estimates of heterosis genetic effects on birth weight are presented in table 13. Crosses involving the Brahman breed had the largest estimates (5.8 to 6.5 kg, $P<.01$) of direct heterosis effects on BWT. These results were generally in agreement with those of Vaamonde and Franke

(1984) and Wyatt and Franke (1986) relative to the IhAB effect and those of Vaamonde and Franke (1984), Roberson et al. (1986), Wyatt and Franke (1986) and Comerford et al. (1987) relative to the IhBH effect for BWT. These results were, however, different from those of Wyatt and Franke (1986) relative to the IhBC effect for BWT.

Charolais-British and British-British crosses generally had smaller estimates of direct heterosis effects for BWT (-1.9 to 2.8 kg) than crosses involving the Brahman breed. The IhAC effect on BWT was similar to that reported by Wyatt and Franke (1986). The IhCH effect on BWT of 2.8 kg ($P<.05$) was in direct contrast to the negative value reported by Wyatt and Franke (1986). Other studies have reported nonsignificant direct heterosis effects of the Charolais-British crosses on BWT (Alenda et al., 1980; Dillard et al., 1980). The IhAH effect on BWT of 2.6 kg ($P<.01$) was larger than those reported in the literature (Gregory et al., 1978b; Alenda et al., 1980; Dillard et al., 1980; Vaamonde and Franke, 1984; Koch et al., 1985; Morris et al., 1986; Wyatt and Franke, 1986).

Brahman crosses demonstrated negative maternal heterotic influences on birth weight (-3.9 to -2.0 kg). These estimates were different from the positive values reported for crosses among the Brahman and British breeds by some researchers (Vaamonde and Franke, 1984; Roberson et al., 1986; Wyatt and Franke, 1986).

TABLE 13. DIRECT AND MATERNAL HETEROSIS EFFECTS FOR BIRTH WEIGHT (kg)[a]

	Breed			
Breed	Angus	Brahman	Charolais	Hereford
Angus		5.8±1.3** (1,128)[b]	-1.9±1.2+ (554)	2.6±.9** (591)
Brahman	-2.3±1.1* (1,128)		6.5±1.3** (1,107)	5.8±1.3** (1,189)
Charolais	1.3±1.2 (554)	-3.9±1.1** (1,107)		2.8±1.1* (558)
Hereford	.8±.9 (591)	-2.0±1.2+ (1,189)	.5±1.0 (558)	

[a]Direct and maternal heterosis effects are above and below the diagonal, respectively.
[b]Figures in brackets represent number of observations.
**P<.01.
*P<.05.
+P<.10.

The estimate of the MhAC effect for BWT (1.3 kg) was similar to those reported by Alenda et al. (1980), Knapp et al. (1980) and Wyatt and Franke (1986). The estimate of the MhCH effect for BWT (.5 kg) was similar to those reported by Alenda et al. (1980) and Knapp et al. (1980) but smaller than the 1.8 kg reported by Wyatt and Franke (1986). The estimate of the MhAH effect for BWT was small but positive (.8 kg). This generally agreed with the results reported by Vaamonde and Franke (1984), Koch et al. (1985) and Morris et al. (1986). This estimate was, however, different from the negative values of the MhAH effect for BWT reported by Alenda et al. (1980), Knapp et al. (1980) and Wyatt and Franke (1986).

In summary, Brahman crosses were associated with the largest direct and the lowest maternal heterosis effects for BWT. The AH and CH crosses were similar in their direct and maternal heterotic effects on BWT. The AC breed combination demonstrated the smallest direct and the greatest maternal heterotic influence on BWT.

Preweaning ADG. Presented in table 14 are the least-squares partial regression coefficients which correspond to the estimates of the direct and maternal additive genetic effects for the ADG. Estimates of the IgC and MgC effects for ADG were .07 and .05 kg/d ($P<.01$), respectively. The IgC and MgC effects for ADG were .07 and .17 kg per day, respectively, more than those of Hereford.

TABLE 14. BREED DIRECT AND MATERNAL ADDITIVE EFFECTS FOR ADG (kg/day)

Breed	Additive effects	
	Direct b±SE[a]	Maternal b±SE
Angus	-.034±.012**	-.014±.012
Brahman	-.047±.017**	.070±.017**
Charolais	.074±.013**	.051±.013**
Hereford	.008±.011	-.107±.011**

**P<.01.
*P<.05.
[a]Partial regression coefficient and standard error.

Dillard et al. (1980) reported similar estimates of IgC and MgC effects for ADG relative to the Hereford. When compared to the IgA effect, the larger IgC effect for ADG of .11 kg was similar to the .12 kg reported by Wyatt and Franke (1986) while that of the MgC component (.07 kg) was more than the .03 kg obtained by Wyatt and Franke (1986).

The estimate of the IgB effect for ADG was -.047 kg/d (P<.01) while that of the MgB component was .07 kg/d (P<.01). When compared to that of the Angus breed, the IgB effect decreased ADG by .02 kg while the MgB effect increased ADG by .08 kg per day. Similar results for BWT were obtained in other studies by comparing the IgB effect to the IgA effect (Vaamonde and Franke, 1984; Wyatt and Franke, 1986). The IgB effect on ADG was .06 kg/d less than that of Hereford while the MgB effect was .18 kg/d more than that of Hereford. Roberson et al. (1986) found also positive but smaller estimates for the IgB and MgB effects on ADG relative to the Hereford.

The estimates of IgA and MgA effects for ADG were -.03 (P<.01) and -.01 kg per day while those of IgH and MgH effects were .01 and -.11 (P<.01) kg per day, respectively. Estimates of IgA and MgA effects for ADG were, respectively, -.04 and .09 kg/d compared to those of Hereford. Vaamonde and Franke (1984) and Koch et al. (1985) reported similar results for ADG when comparing IgA and MgA effects with those of Hereford, respectively. Gregory et al. (1978b), Dillard et al. (1980) and Morris et al. (1986) found similar estimates for the MgA effect on ADG relative to the Hereford. They, however, found a positive advantage of the IgA effect for ADG over that of Hereford. Morris et al. (1986) and Wyatt and Franke (1986) found nonsignificant differences between the IgA and IgH effects on ADG. The results of this study tend to support the observation that Angus dams generally have a maternal advantage over Hereford dams. There was no apparent conclusive evidence of the greater transmitting ability of Hereford relative to the Angus in the growth of their calves to weaning.

In this study, C and B breeds demonstrated superior maternal advantage over the British breeds for ADG, with H having the smallest maternal effect. The C breed also manifested the largest direct genetic effect for the growth rate of their calves while B had the smallest potential for their calf growth to weaning. The A and H breeds were intermediate in direct additive genetic effects for the growth of their calves to weaning.

Least-squares estimates of direct and maternal heterosis effects on ADG are presented in table 15. The Brahman cross direct heterosis effects were generally significant and positive for ADG. Estimates of the IhAB and IhBH effects for ADG were .16 and .13 kg/d ($P<.01$), respectively. These results were in general agreement with those of Vaamonde and Franke (1984) and Wyatt and Franke

TABLE 15. DIRECT AND MATERNAL HETEROSIS EFFECTS FOR ADG (kg/day)[a]

	Breed			
Breed	Angus	Brahman	Charolais	Hereford
Angus		.161±.026**	.052±.024*	.044±.018**
Brahman	.012±.023		.126±.026**	.133±.026**
Charolais	.039±.023+	.002±.022		.064±.023**
Hereford	.069±.019**	.071±.023**	.058±.021**	

[a]Direct and maternal heterosis effects are above and below the diagonal, respectively.
**P<.01.
*P<.05.
+P<.10.

(1986). The estimate of the IhBH effect for ADG was, however, greater than the .02 kg reported by Roberson et al. (1986) in a Texas study. Differences among these results could be due partly to the variation in the environments (Barlow, 1981) and partly to sampling errors in these studies.

Estimates of the MhAB and MhBH effects for ADG were .01 and .07 (P<.01) kg per day, respectively. Vaamonde and Franke (1984) and Wyatt and Franke (1986) found similar estimates for the MhBH effect on ADG. This estimate of the MhBH effect on ADG was greater than the .02 kg/d (P<.01) reported by Roberson et al. (1986). Vaamonde and Franke (1984) and Wyatt and Franke (1986) reported greater estimates for the MhAB effect on ADG (.05 to .09 kg/d) than the .01 kg/d found in this study.

Estimates of IhBC and MhBC effects for ADG were, respectively, .13 (P<.01) and .00 kg per day. The IhBC contribution to ADG was larger than the .09 kg per day (P<.01) reported by Wyatt and Franke (1986). Crosses among C and British breeds produced significant, positive direct heterosis effects on ADG. Direct and maternal heterosis effects on ADG due to the AC and CH breed combinations ranged from .05 to .06 and .04 to .06 kg per day, respectively. These results were different from those of Dillard et al. (1980) and Wyatt and Franke (1986) for the IhAC effect and from Wyatt and Franke (1986) for the IhCH effect on ADG. These researchers found approximately the same estimates (.01 kg/d) for the IhAC effect on ADG. Dillard et al. (1980) found a .05 kg ($P<.05$) advantage of the IhCH effect for ADG compared to the .01 kg reported by Wyatt and Franke (1986). The MhAC effect on ADG was barely significant while that of the CH breed combination significantly influenced ADG. Similar trends for these effects on ADG were reported by Wyatt and Franke (1986), although their estimates were smaller than those observed in this study. Knapp et al. (1980), however, reported a negative estimate of the MhAC effect and a positive estimate of the MhCH effect for ADG, although their estimates were nonsignificant.

The AH breed combination had significant positive direct and maternal heterosis effects on ADG (.04 and .07 kg/d, $P<.01$, respectively). Similar trends for these effects on ADG were reported in the literature (Gregory et al., 1978b; Dillard et al., 1980; Knapp et al., 1980; Vaamonde and Franke, 1984; Koch et al., 1985; Morris et al., 1986; Wyatt and Franke, 1986). However, most of the estimates for the IhAH and MhAH effects for ADG (.01 to .03 and .01 to .06 kg/d, respectively) reported were less than those obtained in this study.

Summarizing, Brahman crosses had the largest direct heterosis effects on ADG. On the contrary, Brahman crosses, with the exception of BH cross, had the least maternal heterosis influence on ADG. The AC, AH and CH breed combinations had generally similar estimates of direct and maternal heterosis effects for ADG. In most cases, only breed combinations involving H demonstrated significant and large maternal heterosis influences on ADG.

Weaning Weight. Least-squares estimates for the direct and maternal additive genetic effects for weaning weight are presented in table 16. The C breed had the largest estimates of direct and maternal additive genetic effects for WWT. These IgC and MgC effects increased WWT by 22 and 13 kg ($P<.01$), respectively. Peacock et al. (1981) reported a 30 kg increase for the IgC effect on WWT. Alenda et al. (1980) and MacNeil et al. (1982) obtained estimates ranging from 12 to 13 kg for the IgC effect on WWT. For the MgC effect on WWT, a similar estimate was reported by Alenda et al. (1980) and MacNeil et al. (1982). A negative estimate (-6.1 kg) was reported by Peacock et al. (1981). The 34 kg advantage of the IgC effect on WWT over the IgA effect was smaller than the 42 kg reported by Wyatt and Franke (1986). On the contrary, the C breed manifested a 15 kg maternal superiority over Angus for WWT compared to the 4 kg reported by Wyatt and Franke (1986). The IgC and MgC effects were also greater than those of H by 22 and 36 kg, respectively, for WWT. Dillard et al. (1980) found similar results for the IgC and MgC effects on WWT relative to the Hereford.

Estimates of IgB and MgB effects for WWT were -9.6 kg

TABLE 16. BREED DIRECT AND MATERNAL ADDITIVE EFFECTS FOR WEANING WEIGHT (kg)

	Additive effects	
Breed	Direct b±SE[a]	Maternal b±SE
Angus	-12.3±2.9**	-1.8±2.9
Brahman	-9.6±4.2*	11.7±4.1**
Charolais	22.1±3.1**	13.1±3.1**
Hereford	-.3±2.8	-23.0±2.8**

**P<.01.
*P<.05.
[a]Partial regression coefficient and standard error.

(P<.05) and 11.7 kg (P<.01), respectively. Peacock et al. (1981) reported a similar estimate for the MgB effect on WWT but a smaller estimate for the IgB effect. The IgB effect for WWT was 9.3 kg less than that of Hereford and 2.7 kg more than that of Angus. The MgB effect for WWT was 34.7 and 13.5 kg, respectively, more than that of Hereford and Angus. Similar results were apparent for the IgB and MgB effects on WWT compared to those of Hereford (Roberson et al., 1986). Vaamonde and Franke (1984) and Wyatt and Franke (1986) found that the IgB effect on WWT was 13.0 and 3.0 kg, respectively, more than that of Angus while the MgB effect was -.20 and 3.7 kg, respectively, less or more than that of Angus. Variation in these results could be due partly to differences in the breeding structure among these studies (Cunningham, 1987) and partly to sampling errors.

The IgA and MgA effects for WWT were, respectively, -12.3 (P<.01) and -1.8 kg. Similar results for WWT were reported by Alenda et al. (1980) and Peacock et al. (1981). MacNeil et al. (1982) reported a similar value for the IgA effect and a nonsignificant, positive estimate for the MgA effect on WWT. Gaines et al. (1970) reported large negative IgA and positive MgA effects on WWT from an analysis of a diallel mating design involving Angus, Hereford and Shorthorn breeds. Their estimates were, however, associated with large standard errors.

The IgA effect on WWT was 12.0 kg less than that of

Hereford while the MgA component was 21.2 kg more than that of Hereford. Vaamonde and Franke (1984) reported a similar difference between the IgA and IgH effects for WWT compared to the -5.4 to -1.6 kg difference for A-H reported by Dillard et al. (1980), Koch et al. (1985), Morris et al. (1986) and Wyatt and Franke (1986). They, however, reported smaller differences between the MgA and MgH effects for WWT (9.5 to 13.0 kg) than that observed in this study. In contrast, Gregory et al. (1978b) reported a 5.0 kg increase in WWT for the IgA effect relative to the Hereford.

Estimates of the IgH and MgH effects for WWT were -.3 and -23.0 ($P<.01$) kg, respectively. These estimates were different from those reported in the literature (Alenda et al., 1980; MacNeil et al., 1982). Gaines et al. (1970) found 12.3 kg Ig(H-A) and -23.5 kg Mg(H-A) effects on WWT based on a diallel analysis involving Angus, Hereford and Shorthorn breeds.

MacNeil et al. (1982) found that the IgH effect was less than that of Angus and the MgA effect was less than that of Charolais and greater than that of Hereford for 205 day weight. Many studies have reported the maternal superiority of the Angus over the Hereford breed of dam (Smith et al., 1976; Gregory et al., 1978b, 1979). Knapp et al. (1980) observed that the MgC effect was greater than that of Angus for 205 day weight.

In summary, the C breed had the greatest direct additive effect on WWT while IgA effect was the least. The B and H breeds were intermediate in direct additive effect on WWT. Charolais and B had the largest maternal additive effect on WWT; MgA effect was intermediate and that of H was the least.

Estimates of heterotic genetic effects for weaning weight are shown in table 17. The Brahman-British direct heterosis effects significantly influenced WWT. Estimates of the IhAB and MhAB effects for WWT were 41.8 ($P<.01$) and .6 kg while those of IhBH and MhBH effects were 35.4 ($P<.01$) and 13.9 ($P<.05$) kg, respectively. Relative to the maternal heterotic effects, only the MhBH effect increased WWT ($P<.05$). The estimate of the IhAB effect on WWT was larger than those reported by most researchers (Peacock et al., 1981; Vaamonde and Franke, 1984; Wyatt and Franke, 1986) while the estimate of the MhAB effect was smaller than those reported by these same workers. Estimates of IhBH and MhBH effects on WWT were approximately the same as those in the scientific literature (Vaamonde and Franke, 1984; Roberson et al., 1986; Wyatt and Franke, 1986).

Estimates of IhBC and MhBC effects on WWT were 34.3 ($P<.01$) and -3.6 kg, respectively. The IhBC effect on WWT was larger than those reported by Peacock et al. (1981) and Wyatt and Franke (1986). The MhBC effect on WWT was nonsignificant and negative in contrast to the 18.7 kg ($P<.01$) reported by Peacock et al. (1981).

TABLE 17. DIRECT AND MATERNAL HETEROSIS EFFECTS FOR WEANING WEIGHT (kg)[a]

	Breed			
Breed	Angus	Brahman	Charolais	Hereford
Angus		41.8±6.4**	10.2±5.9+	12.9±4.4**
Brahman	.6±5.6		34.3±6.3**	35.4±6.4**
Charolais	10.0±5.7+	-3.6±5.5		18.3±5.6**
Hereford	16.5±4.6**	13.9±5.7*	13.5±5.1**	

[a]Direct and maternal heterosis effects are above and below the diagonal, respectively.
**P<.01.
*P<.05.
+P<.10.

Breed and environmental differences across the different studies (Barlow, 1981) and possible sampling errors might have partially contributed to the variability in these results.

Among the Charolais x British crosses, only the CH combination showed significant positive direct and maternalheterotic influences on WWT. The AC combination manifested slight direct and maternal heterotic effects on WWT. Estimates of the IhAC and MhAC effects for WWT were about the same (10.2 vs 10.0 kg) while those of the IhCH and MhCH effects were 18.3 and 13.5 kg ($P<.01$), respectively. Alenda et al. (1980) found a similar estimate of the IhAC effect for WWT. In contrast, Dillard et al. (1980), Peacock et al. (1981) and Wyatt and Franke (1986) reported lower estimates, ranging from -.9 to 3.7 kg, for the IhAC effect on WWT. Alenda et al. (1980) and Peacock et al. (1981) found larger estimates of MhAC effects for WWT (15.2 to 16.5 kg) than those reported in this study. The estimate of the MhAC effect for WWT was larger than those reported by Knapp et al. (1980) and Wyatt and Franke (1986). Estimates of the IhCH and MhCH effects for WWT were larger than those reported by most researchers (Alenda et al., 1980; Dillard et al., 1980; Knapp et al., 1980; Wyatt and Franke, 1986).

Angus-Hereford direct and maternal heterosis effects had significant positive influences on WWT. Estimates of the IhAH and MhAH effects for WWT were 12.9 and 16.5 kg ($P<.01$), respectively. Similar trends were reported by Gregory et al. (1978b) and Dillard et al. (1980) for the IhAH effect and by Vaamonde and Franke (1984), Koch et al. (1985), Morris et al. (1986) and Wyatt and Franke (1986) for the IhAH and MhAH effects on WWT. Alenda et al. (1980) reported negative estimates for the IhAH and MhAH effects on WWT.

Summarizing, Brahman crosses had the largest estimates of direct heterosis effects for WWT. The AB and BC breed combinations had the least maternal heterotic influence on WWT. The maternal heterosis effect on WWT due to the BH breed combination was similar to those of CH and AC breed combinations but smaller than that of the AH breed combination. The AC and AH crosses had the lowest estimates of direct heterosis effects for WWT while that of CH breed combination was intermediate. The results of this study do not appear to support the finding that AH crosses tended to produce relatively lower heterosis for weaning traits than other contemporary breeds (Cundiff, 1970; McDonald, 1972; Long and Gregory, 1974; Crockett et al., 1978). However, these results do suggest that A and H breeds are genetically related breeds. They also suggest that C and the British breeds (<u>Bos taurus</u> breeds) are genetically more related than the B (<u>Bos indicus</u> breed).

<u>Condition Score</u>. Weaning condition score may reflect to some extent thriftiness and vitality in the offspring under unfavorable environmental conditions (Koger et al., 1975).

This trait may also vary over time because of the subjective evaluation of the calf at weaning and the potential variance in the evaluation criteria. Least-squares regressions corresponding to the direct and maternal additive genetic effects on condition score (SCORE) are presented in table 18.

The estimate of the IgH effect for SCORE was the largest (.73 units, P<.01) while the MgH component was the smallest (-.95 units, P<.01). The IgA and IgH effects on SCORE were larger than the IgB and IgC effects, with the IgC effect being intermediate. On the contrary, MgB and MgC effects on SCORE were larger than MgA and MgH effects, with the MgA effect being intermediate. Estimates of IgA and MgA effects on SCORE were .37 (P<.01) and -.02 units, respectively. These estimates were larger than the .13 and -.11 units, respectively, reported by Peacock et al. (1981) in a Florida study. The IgA effect on SCORE was .36 units less than that of Hereford while the MgA effect was .93 units more than that of Hereford. Dillard et al. (1980) reported a similar pattern for the maternal additive genetic difference between the Angus and Hereford breeds. They, however, found that the IgA effect on SCORE was .29 units more than that of Hereford. Gaines et al. (1970) found that IgA and MgA effects on SCORE were, respectively, .47 and .36 units more than those of Hereford based on a diallel analysis involving Angus, Hereford and Shorthorn breeds.

TABLE 18. BREED DIRECT AND MATERNAL ADDITIVE EFFECTS FOR CONDITION SCORE (grade units)

	Additive effects	
Breed	Direct b±SE[a]	Maternal b±SE
Angus	.37±.14**	-.02±.14
Brahman	-.62±.20**	.58±.20**
Charolais	-.48±.15**	.39±.15**
Hereford	.73±.14**	-.95±.13**

**P<.01.
*P<.05.
[a]Partial regression coefficient and standard error.

Estimates of IgB and IgC effects on SCORE were -.62 and -.48 units (P<.01), respectively. In contrast, the estimates of MgB and MgC effects on SCORE were .58 and .39 units (P<.01), respectively. Peacock et al. (1981) found a nonsignificant increase in SCORE as a consequence of the MgB effect and a significant decrease due to the IgB effect. Peacock et al. (1981) reported small and nonsignificant estimates of the IgC and MgC effects on SCORE. The IgH effect on SCORE was more than the IgC effect by 1.21 units while the MgC effect was more than that of Hereford by 1.34 units. Dillard et al. (1980) observed a similar difference between the maternal genetic effects of C and H for SCORE. However, they found a positive advantage of the IgC over the IgH effect for SCORE.

In this study, the H breed had the largest direct additive effect on SCORE. The inheritance of A tended to increase SCORE while that of B and C tended to decrease it. Meanwhile, the maternal ability of B and C increased SCORE and that of A and H decreased it.

Estimates of the direct and maternal heterosis effects for weaning condition score are shown in table 19. Brahman x British crosses demonstrated significant positive and generally large direct heterosis effects on SCORE. Estimates of the IhAB and MhAB effects for SCORE were .98 (P<.01) and -.09 units while those of the BH breed combination were .86 (P<.01) and .47 (P<.10) units, respectively.

TABLE 19. DIRECT AND MATERNAL HETEROSIS EFFECTS FOR CONDITION SCORE (grade units)[a]

	Breed			
Breed	Angus	Brahman	Charolais	Hereford
Angus		.98±.31**	.12±.28	.13±.21
Brahman	-.09±.27		.52±.31+	.86±.31**
Charolais	.14±.28	-.05±.26		.45±.27+
Hereford	.77±.22**	.47±.28+	.56±.25*	

[a]Direct and maternal heterosis effects are above and below the diagonal, respectively.
**P<.01.
*P<.05.
+P<.10.

Peacock et al. (1981) reported a similar value for the IhAB effect on SCORE. However, they found a .94 unit ($P<.01$) increase in SCORE due the MhAB effect in contrast to the nonsignificant and negative estimate observed in this study. Differences in maternal heterosis effects on SCORE could partly reflect differences in environmental conditions and partly relate to sampling errors for these studies.

Estimates of the IhBC and MhBC effects on SCORE were .52 ($P<.10$) and -.05 units, respectively. Peacock et al. (1981) reported significant increases in SCORE due to the IhBC effect. However, unlike in this study, they found significant increases in SCORE due to the MhBC effect. Estimates of IhAC and MhAC effects for SCORE were .12 and .14 units while those of the CH breed combination were .45 ($P<.10$) and .56 ($P<.05$) units, respectively. This same trend was observed by Dillard et al. (1980) for the IhAC and IhCH effects on SCORE. Peacock et al. (1981) found increases in SCORE due to the effects of the IhAC and MhAC components. However, Knapp et al. (1980) reported a decrease in SCORE of .40 units due to the MhAC effect and a zero estimate relative to the MhCH effect.

Estimates of the IhAH and MhAH effects for SCORE were .13 and .77 ($P<.01$) units, respectively. The IhAH effect on SCORE was about equal to the .15 units reported by Dillard et al. (1980). Knapp et al. (1980) found a similar estimate for the MhAH effect on SCORE, although this was nonsignificant.

General Discussion

Angus, H and B breeds had generally low Ig estimates for all preweaning traits except SCORE in this study. The C had generally the largest Ig estimates for all preweaning traits except SCORE. Estimates of IgB and IgH effects for all preweaning traits except SCORE were larger than that of Angus. However, Angus had the largest maternal additive breed effect on BWT and a relatively large direct additive breed effect on SCORE. These observations were generally in agreement with those of Alenda et al. (1980) relative to A, H and C. This was as expected considering the general characteristics and evolutionary history of these breeds (Marshall et al., 1976; Roberson et al., 1986). The results of this study also confirm the importance of maternal genetic effects for the preweaning growth traits (Gregory et al., 1965; Brown and Galvez, 1969; Turner, 1969; Koch, 1972; Gaines et al., 1978; Ellis et al., 1979).

The additive genetic effect (or additive breed effect) is characteristic of each breed for a specific trait. It is due to the accumulation of favorable additive effects at a large number of independent loci (Cunningham, 1987). Dickerson (1969) and Chapman and Franke (1987) stated that breed differences arise partly from natural and artificial selection for adaptability and productivity under differing environmental conditions and partly from random cumulative genetic changes over time. Breed differences for preweaning traits have been clearly evident in this study.

Brahman crosses had generally larger estimates of direct heterosis effects for the preweaning traits than the AC and CH crosses (Wyatt and Franke, 1986). Vaamonde and Franke (1984) also found that Brahman crosses had large estimates of direct heterosis effects for preweaning traits. The CH cross had a tendency to exert larger direct heterosis effect on all preweaning traits than the AC cross. A similar trend for the C and British crosses was observed for the maternal heterosis influence on all preweaning traits except BWT. Angus-Hereford crosses generally demonstrated relatively low direct heterosis influences on all preweaning traits except BWT. Hereford crosses manifested the greatest maternal heterosis effects for all preweaning traits except BWT. These differences could be explained partly by the slower growth rate of the Angus and Brahman than the Charolais breeds (Peacock et al., 1981) and partly by the degree of diversity among the breeds involved (Dickerson, 1969, 1973; Chapman and Franke, 1987). Probably any differences in inbreeding levels among these breeds could also have contributed to the variation in these results.

Any observed differences between this study and others from the scientific literature may reflect partly the within-breed sampling of sires used and partly differences in environmental conditions under which the respective studies were conducted. These differences could also reflect the effect of genotype by environment interaction. Genotype by environment interactions have been reported to account for biases among estimates of heterosis effects (Barlow, 1981; Sprague, 1983). Hohenboken (1985) noted, in summarizing genotype by environment interactions, that the amount of heterosis from crossing two or more breeds could vary with the environmental conditions to which the population was exposed. Brinks and Knapp (1975) found that reductions in ADG of Hereford calves caused by inbreeding of the dam was twice as great in males as in females. Keller and Brinks (1978) reported that inbreeding depression on WWT of beef calves was more pronounced under conditions of environmental stress. Young (1971) also observed that hybrid vigor was greatest under more stressful conditions for growth and least under optimum conditions.

Conclusion

The C had the largest Ig estimate for BWT, ADG and WWT while H had the largest Ig estimate for SCORE. Angus and C had similar and larger Mg estimates for BWT than H and B. Angus and B had the lowest Ig and Mg estimates, respectively, for BWT. Brahman and C had similar and larger Mg estimates for ADG, WWT and SCORE than A and H. The H had the lowest Mg estimate for ADG, WWT and SCORE.

Brahman crosses (AB, BC and BH) had the largest Ih estimates for all preweaning traits. Brahman crosses had also the lowest Mh estimates for BWT. Except for the BH combination, Brahman crosses also had the lowest Mh estimates for ADG, WWT and SCORE. Hereford crosses (AH, CH and BH) had the largest Mh estimates for all preweaning traits except BWT.

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CHAPTER III

AN APPLICATION OF GENETIC EFFECTS TO THE PREDICTION OF PREWEANING PERFORMANCE FOR CROSSES FROM DIFFERENT MATING SYSTEMS

Summary

Estimated direct (Ig) and maternal (Mg) additive and direct (Ih) and maternal (Mh) heterotic genetic parameters from Chapter II were fitted to a prediction equation to estimate the preweaning performance of each genetic group in a breeding system. The expected average preweaning performance for progeny was computed as a deviation from the overall mean for each preweaning trait. Preweaning traits considered included birth weight (BWT), preweaning average daily gain (ADG), weaning weight (WWT) and condition score (SCORE). The prediction model included each genetic effect multiplied by the corresponding proportion of genes or loci contributed by the respective breed or breed combination to the formation of each offspring. This model was based on the assumption that the expected average performance is a linear combination of the genetic effects. Breeds considered included Angus (A), Brahman (B), Charolais (C) and Hereford (H) and mating systems examined involved straightbreeding, two- and three-breed terminal crossing, backcrossing and two-, three- and four-breed rotational crossbreeding. These results suggested that direct and maternal additive genetic

effects and direct heterotic effects contributed significantly to variation in birth weight. These results imply, therefore, that matings can be designed to partially control calving problems. Condition score was affected mostly by direct and maternal additive genetic effects. Direct and maternal additive and heterotic genetic effects were important for ADG and WWT. Breeds with large direct additive genetic effects (e.g., C) tended to produce larger ADG and WWT constants for backcross than for two- and three-breed terminal cross calves. Breeds with positive maternal genetic effects (e.g., B and C) and serving as dams were associated with large ADG and WWT constants for two-breed terminal cross calves. Direct heterosis effects of Brahman crosses contributed significantly to large ADG and WWT constants for two- and three-breed terminal cross calves. Two- and three-breed backcross calves with increasing B and C inheritance tended to gain faster and become heavier at weaning than those with increasing A and H inheritance. Among the rotational systems in cyclic equilibrium, those crosses with breeds having large direct and maternal additive genetic effects and with breed combinations having large direct heterosis effects (e.g., Brahman crosses) tended to have large predicted ADG and WWT. Crosses with A or H breeding had larger SCORE at weaning than those with B or C breeding. In general, heterosis effects were not important for SCORE except for crosses that contained AB or

BH breed combinations and those with crossbred dams having the AH genotype.

(Key Words: Prediction Model, Stabilized Rotational Crosses, Terminal Crosses, Backcrosses).

Introduction

Animal breeders often must design long-term breeding experiments that can provide livestock producers with information to assist them in selecting breed resources and mating systems that will maximize production efficiency. Estimates of direct and maternal additive and heterotic genetic effects should help to overcome this period of waiting frequently for research results by providing the breeder with useful information for (1) making predictions of the performance of crosses of interest without actually producing and testing all of them, (2) selecting breeds for use in a crossbreeding program and (or) modifying the sequence of breeds entering a rotational crossing system, or (3) evaluating and selecting effective and efficient breeding systems (Robison et al., 1981). The theory of breed utilization, as developed by Hill (1971), Dickerson (1969, 1973) and Robison et al. (1981), provides a basis for predicting the performance of any mating group under the assumption that the genetic parameters are adequately known.

The choice of breed combinations and of mating systems that will maximize calf performance requires the simultaneous consideration of direct and maternal additive and heterotic genetic effects for each economically important trait. MacNeil et al. (1982) proposed that breeds with large estimates of direct additive genetic effects should be most suitable as sire breeds while those with high maternal additive genetic effects should be most useful as dam breeds for most crossbreeding schemes.

The objective of this study was to evaluate the preweaning performance of four breeds (Angus, Brahman, Charolais and Hereford) in 8 breeding systems. Straightbred, two- and three-breed terminal, two- and three-breed backcross and two-, three- and four-breed rotational crosses were produced. Previously estimated genetic parameters (Chapter II) and a prediction model were used in evaluating these breed groups.

Materials and Methods

Data for this study consisted of estimates of direct and maternal additive and heterotic genetic parameters for the four breeds (Angus, Brahman, Charolais and Hereford) and their crosses. These estimates were obtained using data that were described in Chapter II. Preweaning traits including birth weight, preweaning ADG, weaning weight and condition score were used as a basis on which to evaluate the breeding groups. The expected average performance of a straightbred or crossbred individual was expressed as a linear function of breed direct and maternal additive genetic effects for the straightbreds, as well as direct and (or) maternal heterosis effects for the crossbreds (Dickerson, 1969, 1973).

The assumptions in the estimation procedure were that: (1) data were a random sample of the populations; (2) there is a linear and additive relationship among the genetic parameters; (3) there are no other genetic effects besides those included in the models; and (4) environmental conditions were consistent across breeding groups. The prediction models used for this analysis are as follows:

Model I (used to estimate constants for all mating systems other than the stabilized rotational system):

LSC = (fA)(IgA) + (fB)(IgB) + (fC)(IgC) + (fH)(IgH)
+ (fAB)(IhAB) + (fAC)(IhAC) + (fAH)(IhAH) + (fBC)(IhBC)
+ (fBH)(IhBH) + (fCH)(IhCH) + (f'A)(MgA) + (f'B)(MgB)
+ (f'C)(MgC) + (f'H)(MgH) + (f'AB)(MhAB) + (f'AC)(MhAC)
+ (f'AH)(MhAH) + (f'BC)(MhBC) + (f'BH)(MhBH)
+ (f'CH)(MhCH),

where,

LSC = Breed group least-squares constant (a deviation of the expected average performance from the overall mean),

Igi = direct additive genetic effect due to the ith breed (i = A, B, C, or H),

Mgi = maternal additive genetic effect due the ith dam breed (i = A, B, C, or H),

fi and f'i = proportion of ith breed in the calf and dam genotypes, respectively,

fij and f'ij = proportion of heterozygous loci with genes from ijth breed combinations, respectively, in the calf and dam genotypes (i # j),

Ihij = direct heterosis effect due to ijth breed combinations (AB, AC, AH, BC, BH or CH) in the calf genotype,

Mhij = maternal heterosis effect due to ijth breed combinations (AB, AC, AH, BC, BH or CH) in the genotype of the dam of the calf.

Examples: The predictive model for:

(1) Straightbred : LSC(i) = Igi + Mgi;

(2) Two-breed terminal cross:

LSC(ij) = 1/2Igi + 1/2Igj + Mgj + Ihij;

(3) Two-breed backcross:

LSC(ij) = 3/4Igi + 1/4Igj +1/2Mgi + 1/2Mgj + 1/2Ihij + Mhij;

and

(4) Three-breed cross:

LSC(ijk) = 1/2Igi + 1/4Igj + 1/4Igk + 1/2Mgj

$+ 1/2Mgk + 1/2Ihij + 1/2Ihik + Mhjk.$

At equilibrium all dams and progeny in a rotational system are crossbred and consequently benefit from both the direct and maternal heterosis effects. Rotational crossbreeding systems attain cyclic equilibrium within 4 to 6 generations with the following types of animals:

a) two types of grades (1/3 and 2/3) for the two-breed rotation coexisting in cyclic equilibrium, with a maximum heterosis equal to 67 percent of the heterozygosity of the F1 generation,

b) three types of grades (1/7, 2/7 and 4/7) for the three-breed rotation coexisting in cyclic equilibrium, with a maximum 86 percent of the heterosis in the F1 generation, and

c) four types of grades (1/15, 2/15, 4/15 and 8/15) for the four-breed rotation coexisting in cyclic equilibrium, with a maximum heterosis equal to 93 percent of the F1 generation (Dickerson, 1969; Alenda et al., 1980).

Therefore, predicted constants for the stabilized rotational crossbreeding system were expressed a function of the following genetic expectations (model II):

$$LSC(2BRij) = 1/2Igi + 1/2Igj + 1/2Mgi + 1/2Mgj + 2/3Ihij + 2/3Mhij,$$

$$LSC(3BRijk) = 1/3Igi + 1/3Igj + 1/3Igk + 1/3Mgi + 1/3Mgj + 1/3Mgk + 2/7Ihij + 2/7Ihik + 2/7Ihjk + 2/7Mhij + 2/7Mhik + 2/7Mhjk,$$

$$LSC(4BRijkl) = 1/4Igi + 1/4Igj + 1/4Igk + 1/4Igl + 1/4Mgi + 1/4Mgj + 1/4Mgk + 1/4Mgl + 7/45Ihij + 7/45Ihik + 7/45Ihil + 7/45Ihjk + 7/45Ihjl + 7/45Ihkl + 7/45Mhij + 7/45Mhik + 7/45Mhil + 7/45Mhjk + 7/45Mhjl + 7/45Mhkl,$$

where,

LSC(i) = least-squares constants for two-, three- and four-breed stabilized rotations.

These equations constituted model II that was used to estimate constants for rotational crosses in cyclic equilibrium.

A regression model was employed (SAS, 1982) to obtain predicted least-squares constants for the preweaning traits of straightbred or crossbred progeny produced using various mating systems. These constants represent deviations of the expected average performance of progeny from the overall mean for each preweaning trait.

Results and Discussion

Predicted least-squares constants for preweaning traits of straightbreds, two-, three- and four-breed rotations and two- and three-breed terminal crosses and backcrosses are presented in tables 20 and 21, respectively. Constants of two-, three- and four-breed stabilized rotational crosses are shown in table 22. Predicted least-squares constants

TABLE 20. PREDICTED LEAST-SQUARES CONSTANTS FOR VARIOUS ROTATIONAL CROSSBRED GROUPS

Breed group Sire breed	Dam genotype	Calf preweaning traits: Birth weight (kg)	Preweaning ADG (kg/d)	Weaning weight (kg)	Condition score (units)
mu		33.2	.779	211.3	10.64
Straightbreds					
A	A	-2.4±.3**	-.048±.005**	-14.1±1.2**	.35±.06**
B	B	-3.8±.3**	.023±.006**	2.1±1.4	-.04±.07
C	C	6.8±.3**	.125±.005**	35.2±1.3**	-.10±.06
H	H	- .6±.3*	-.099±.005**	-23.3±1.3**	-.22±.06**
Two-breed rotations					
A	A1B1	-3.6±.5**	.082±.010**	14.9±2.4**	.81±.12**
C	C1B1	2.0±.5**	.169±.009**	40.1±2.3**	.18±.11
H	H1B1	-1.8±.5**	.112±.009**	23.4±2.3**	1.10±.11**
B	A3B1	2.2±.5**	.091±.009**	22.7±2.3**	.58±.11**
B	C3B1	5.3±.5**	.149±.011**	39.0±2.6**	.24±.13+
B	H3B1	2.6±.4**	.046±.008**	13.2±2.0**	.20±.10*
A	B5A3	-2.8±.5**	.109±.009**	21.8±2.2**	.97±.11**
C	B5C3	2.8±.4**	.179±.009**	43.2±2.2**	.27±.10**
H	B5H3	-1.1±.4**	.130±.009**	28.1±2.1**	1.20±.10**
B	A11B5	1.3±.5**	.087±.009**	21.1±2.3**	.51±.11**
B	C11B5	3.9±.5**	.139±.010**	35.3±2.5**	.20±.12+
B	H11B5	1.4±.5**	.043±.011**	11.5±2.6**	.29±.13*
Three-breed rotations					
C	A1B1	.5±.5	.145±.010**	33.4±2.5**	.21±.12+
A	H1B1	-1.9±.5**	.128±.009**	27.1±2.3**	1.05±.11**
C	H1B1	3.3±.5**	.174±.009**	43.2±2.3**	.55±.11**
A	C2A1B1	-1.9±.5**	.117±.010**	24.4±2.4**	.72±.12**
H	A2H1B1	.2±.4	.070±.009**	15.8±2.1**	.99±.10**
H	C2H1B1	1.5±.5**	.128±.010**	30.8±2.5**	1.05±.12**
B	A5C2B1	5.9±.5**	.139±.010**	37.0±2.4**	.66±.12**
B	H5A2B1	4.7±.5**	.086±.010**	24.0±2.4**	.69±.12**
B	H5C2B1	5.8±.4**	.101±.009**	28.6±2.2**	.46±.10**
C	B9A5C2	1.4±.4**	.159±.007**	37.5±1.8**	.25±.09**
A	B9H5A2	-2.1±.4**	.124±.007**	25.9±1.7**	1.04±.08**
C	B9H5C2	3.2±.4**	.177±.007**	43.6±1.7**	.46±.08**
Four-breed rotations					
H	A1B1	- .9±.5*	.111±.010**	24.2±2.4**	.99±.12**
C	H2A1B1	3.5±.5**	.135±.009**	34.8±2.2**	.58±.11**
B	C4H2A1B1	6.8±.5**	.152±.009**	40.9±2.2**	.58±.11**
A	B9C4H2A1	-2.9±.5**	.145±.010**	29.8±2.4**	.99±.12**

**P<.01. *P<.05. +P<.10.

TABLE 21. PREDICTED LEAST-SQUARES CONSTANTS FOR VARIOUS BREED GROUPS

Breed group Sire breed	Dam genotype	Birth weight (kg)	Preweaning ADG (kg/d)	Weaning weight (kg)	Condition score (units)
		Calf preweaning traits			
Two-breed crosses					
A	B	- .3±1.7	.190±.035**	42.6±8.5**	1.44±.41**
A	C	.2±1.3	.123±.026**	28.2±6.5**	.46±.31
A	H	.6±1.0	-.076±.020**	-16.3±4.9**	-.29±.23
B	A	5.7±1.0**	.106±.020**	29.1±5.0**	.84±.24**
B	C	10.9±1.1**	.191±.021**	53.7±5.2**	.36±.25
B	H	6.1±1.0**	.006±.019	7.5±4.7	-.03±.22
C	A	.4±1.3	.057±.025*	13.3±6.2*	.05±.30
C	B	5.1±1.7**	.209±.034**	52.3±8.4**	.55±.40
C	H	5.5±1.1**	-.003±.022	6.3±5.5	-.38±.27
H	A	1.6±1.0	.017±.020	4.9±5.0	.66±.24**
H	B	1.1±1.8	.183±.035**	42.2±8.7**	1.49±.42**
H	C	6.3±1.3**	.155±.026**	42.3±6.5**	.96±.31**
Three-breed crosses					
A	B1C1	-1.0±1.1	.116±.021**	25.0±5.3**	.60±.25+
A	B1H1	1.1± .8	.086±.017**	20.3±4.1**	.75±.20**
A	C1H1	.8±1.0	.081±.020**	19.4±4.9**	.65±.23**
B	A1C1	9.7±1.0**	.187±.020**	51.4±4.8**	.74±.23**
B	A1H1	6.7± .9**	.125±.018**	34.9±4.4**	1.18±.21**
B	C1H1	9.0± .9**	.156±.017**	44.1±4.2**	.73±.20**
C	A1B1	.5± .5	.145±.010**	33.4±2.5**	.21±.12+
C	A1H1	3.7± .8**	.097±.016**	26.4±4.0**	.61±.19**
C	H1B1	3.3± .5**	.174±.009**	43.2±2.3**	.55±.11**
H	A1B1	.4± .5	.129±.010**	29.7±2.5**	.87±.12**
H	A1C1	5.4±1.1**	.113±.022**	31.2±5.5**	.79±.27**
H	C1B1	-1.3± .9	.162±.017**	35.6±4.2**	1.27±.20**

**P<.01.
*P<.05.
+P<.10.

TABLE 21 CONT'D. PREDICTED LEAST-SQUARES CONSTANTS FOR VARIOUS BREED GROUPS

Breed group Sire breed	Dam genotype	Birth weight (kg)	Preweaning ADG (kg/d)	Weaning weight (kg)	Condition score (units)
		Calf preweaning traits			
Two-breed backcrosses					
A	A1C1	.2± .9	.076±.017**	17.0±4.2**	.54±.20**
A	A1H1	- .1± .8	.007±.016	1.4±3.9	.82±.19**
B	B1A1	-1.3± .8	.076±.016**	16.2±4.0**	.31±.19+
B	B1C1	- .4± .8	.108±.016**	24.3±4.0**	.11±.19
B	B1H1	- .9± .8	.085±.017**	18.8±4.1**	.43±.20*
C	C1A1	4.9± .9**	.130±.018**	34.2±4.5**	.11±.22
C	C1H1	6.6± .8**	.119±.017**	34.2±4.1**	.33±.20+
H	H1A1	1.3± .8+	.028±.015	7.4±3.8*	.99±.18**
H	H1C1	3.3± .7**	.086±.015**	23.0±3.6**	.93±.17**
Three-breed backcrosses					
A	A2B1C1	-1.7± .5**	.079±.011**	15.9±2.6**	.68±.12**
A	A2B1H1	-1.9± .5**	.045±.010**	8.1±2.5**	.81±.12**
A	A2C1H1	.1± .6	.042±.013**	9.2±3.2**	.68±.15**
B	B2A1C1	- .8± .8	.092±.016**	20.2±3.8**	.21±.18
B	B2A1H1	-1.1± .8	.080±.016**	17.5±3.9**	.37±.19*
B	B2C1H1	- .6± .8	.097±.016**	21.5±3.9**	.27±.19
C	C2A1B1	3.5± .6**	.149±.011**	37.2±2.7**	.15±.13
C	C2A1H1	5.8± .7**	.124±.014**	34.2±3.5**	.22±.17
C	C2H1B1	4.3± .5**	.144±.010**	37.2±2.5**	.25±.12*
H	H2A1B1	- .2± .5	.070±.010**	15.4±2.4**	1.05±.11**
H	H2A1C1	2.3± .6**	.057±.012**	15.2±2.9**	.96±.14**
H	H2B1C1	.8± .5+	.099±.009**	23.2±2.3**	1.02±.11**

**P<.01.
*P<.05.
+P<.10.

were calculated as deviations from the overall mean for each trait.

<u>Birth Weight</u>. Charolais calves were predicted to be heavier at birth than those of Hereford and Angus breeds. Predicted birth weights of Hereford calves were greater than those of Angus calves while those of Brahman calves were the smallest. These results conform with those of Pahnish et al. (1969), Long and Gregory (1975) and Alenda et al. (1980). The large BWT of straightbred Charolais calves was associated with the large IgC effect while the small BWT of straightbred Brahman calves was attributed to the negative MgB effect.

Brahman-sired two- and three-breed terminal cross calves had the largest BWT while those sired by Angus bulls were the lightest at birth. This behavior can be attributed partly to the large direct heterosis effect of Brahman crosses. The lower BWT associated with Angus-sired calves was due to the small IgA effect for BWT. Straightbred Brahman and Brahman-cross dams produced offspring with relatively low birth weights for two- and three-breed terminal crossing systems. The negative MgB effect and the maternal heterosis effects associated with Brahman crosses partly accounted for these differences (Roberson et al., 1986).

Charolais-sired crossbred calves of two- and three-breed backcrossing systems had the largest predicted BWT while those of Angus and Brahman bulls had the smallest. Hereford-sired backcross calves were intermediate in predicted BWT. The IgA and IgC effects and the Brahman-cross maternal heterosis effects influenced this observation. For the rotational crossbreeding systems, breed combinations with Charolais breeding had the largest predicted BWT while the Brahman-British combinations had the lowest BWT.

These results tended to suggest that direct and maternal additive genetic effects are more important than heterosis effects in the regulation of birth weight. The maternal heterosis effect in these data did not contribute significantly to the variation in birth weight. There was a tendency for the additive and heterotic effects to act in opposite directions for BWT, implying some form of regulatory mechanism for this trait. The regulation of BWT is of prime economic and biological significance to the livestock producer, particularly with respect to calving difficulties and its attendant problems in a breeding herd.

General Discussion

Studies by Bailey and Moore (1980), Gregory et al. (1982) and Roberson et al. (1986) found that Brahman-sired crossbred calves weighed heavier at birth than those sired by British bulls. Birth weights of Brahman-sired crossbred calves were more similar to those of Charolais-sired calves (Barlow and O'Neil, 1980; Gregory et al., 1982; Knox et al., 1982). Ellis et al. (1965) found that the maternal genotype exerted more influence on BWT than the paternal genotype after comparing the birth weights of progeny from Hereford, Brahman and F1 cross cows. Comerford et al. (1987) arrived at a similar conclusion relative to the maternal genotype of the Brahman breed.

The behavior of the Charolais breed tended to support the claim that direct and maternal transmitted effects may be responsible for larger dam breeds producing larger calves at birth than smaller dam breeds (Dickenson, 1954; Joubert and Hammond, 1958; Donald et al., 1962). Cow size may be a limiting factor to the in utero growth of the calf. Fitzhugh et al. (1967), Miquel (1972) and Tawah (1984) reported similar average mature weights for Brahman and Hereford cows which were lower than those of Angus and Charolais cows.

Weaning Traits. Predicted least-squares constants for ADG and WWT are presented in tables 20, 21 and 22 for the different mating systems. For the straightbreds, the Charolais breed had the largest predicted ADG and WWT constants while the Hereford breed had the lowest. Angus and Brahman breeds were intermediate in predicted ADG and WWT constants. There was a large difference in predicted ADG and WWT between Charolais and British breeds. Charolais and Brahman breeds were more alike in predicted ADG and WWT than the British breeds.

TABLE 22. PREDICTED LEAST-SQUARES CONSTANTS FOR TWO-, THREE- AND FOUR-BREED ROTATIONAL COMBINATIONS

Breed group		Calf preweaning traits			
Sire breed	Dam genotype	Birth weight (kg)	Preweaning ADG (kg/d)	Weaning weight (kg)	Condition score (units)
Breed combinations[a]					
Two-breed rotational crosses and combinations					
A	B2A1	-2.5± .6**	.118±.011**	24.1±2.7**	1.02±.13**
B	A2B1	1.0± .5*	.086±.010**	20.5±2.4**	.49±.11**
A-B		- .7± .3*	.102±.006**	22.3±1.6**	.76±.08**
A	C2A1	.2± .7	.092±.013**	20.7±3.2**	.51±.15**
C	A2C1	3.4± .7**	.106±.014**	27.3±3.5**	.09±.17
A-C		1.8± .6**	.099±.012**	24.0±3.0**	.30±.14*
A	H2A1	.1± .6	-.020±.013	-4.5±3.1	.45±.15**
H	A2H1	1.4± .6*	.024±.012*	6.6±3.0*	.88±.14**
A-H		.8± .6	.002±.011	1.0±2.8	.67±.13**
B	C2B1	3.4± .5**	.136±.010**	34.1±2.6**	.19±.12
C	B2C1	3.0± .5**	.182±.011**	44.2±2.6**	.30±.13*
B-C		3.2± .3**	.159±.007**	39.1±1.6**	.25±.08**
B	H2B1	1.4± .5**	.059±.009**	15.0±2.2**	.28±.11**
H	B2H1	- .8± .5	.136±.011**	29.7±2.6**	1.23±.13**
B-H		.3± .3	.097±.006**	22.4±1.5**	.76±.07**
C	H2C1	6.2± .7**	.078±.013**	24.9±3.2**	.09±.15
H	C2H1	4.3± .6**	.109±.013**	29.4±3.1**	.94±.15**
C-H		5.3± .6**	.094±.011**	27.2±2.7**	.52±.13**
Three-breed rotational crosses and combinations					
A	C4B2A1	-2.2± .6**	.130±.012**	27.0±2.9**	.73±.14**
A	B4C2A1	-3.3± .5**	.141±.010**	28.5±2.6**	.95±.12**
B	A4C2B1	6.0± .5**	.144±.011**	38.1±2.6**	.63±.12**
B	C4A2B1	7.0± .6**	.165±.011**	43.9±2.7**	.50±.13**
C	A4B2C1	1.7± .5**	.128±.010**	30.8±2.4**	.16±.12
C	B4A2C1	1.6± .4**	.161±.007**	38.0±1.8**	.25±.09**
A-B-C		1.8± .3**	.145±.006**	34.4±1.4**	.54±.07**
A	H4B2A1	-2.8± .6**	.099±.013**	19.4±3.2**	1.41±.15**
A	B4H2A1	-2.1± .3**	.124±.007**	25.8±1.7**	1.04±.08**
B	H4A2B1	4.5± .5**	.097±.010**	26.4±2.4**	.79±.12**
B	A4H2B1	4.3± .5**	.108±.011**	28.7±2.6**	.89±.13**
H	A4B2H1	.1± .4	.074±.008**	16.6±2.0**	.94±.10**
H	B4A2H1	- .9± .4*	.122±.007**	26.5±1.8**	.92±.06**
A-B-H		.8± .3**	.098±.005**	22.9±1.3**	1.09±.09**
A	H4C2A1	.5± .7	.038±.014**	9.2±3.4**	.57±.16**
A	C4H2A1	.6± .7	.086±.014**	20.0±3.3**	.59±.16**
C	A4H2C1	4.8± .6**	.089±.012**	25.7±2.8**	.39±.14**
C	H4A2C1	3.6± .6**	.100±.012**	26.8±3.0**	.39±.14**
H	C4A2H1	4.9± .7**	.118±.015**	31.8±3.6**	.94±.17**

**P<.01. *P<.05. +P<.10.

TABLE 22 CONT'D. PREDICTED LEAST-SQUARES CONSTANTS FOR TWO-, THREE- AND FOUR-BREED ROTATIONAL COMBINATIONS

Breed group		Calf preweaning traits			
Sire breed	Dam genotype Breed combinations[a]	Birth weight (kg)	Preweaning ADG (kg/d)	Weaning weight (kg)	Condition score (units)
Three-breed rotational crosses and combinations					
H	A4C2H1	3.6± .7**	.082±.014**	22.0±3.5**	.92±.17**
	A-C-H	3.0± .5**	.085±.009**	22.6±2.2**	.63±.11**
B	H4C2B1	5.7± .5**	.155±.009**	31.6±2.3**	.53±.11**
B	C4H2B1	6.6± .5**	.147±.009**	39.8±2.3**	.50±.11**
C	H4B2C1	4.5± .4**	.133±.009**	35.4±2.2**	.36±.11**
C	B4H2C1	3.2± .4**	.177±.007**	43.6±1.7**	.45±.08**
H	C4B2H1	1.7± .6**	.144±.013**	34.7±3.1**	1.08±.15**
H	B4C2H1	- .5± .6	.156±.011**	34.8±2.7**	1.20±.13**
	B-C-H	3.5± .3**	.145±.006**	36.6±1.4**	.69±.07**
Four-breed rotational crosses and combinations					
		**	**	**	**
A	B8C4H2A1	-3.1± .5	.142±.010	29.0±2.4	.96±.11
A	B8H4C2A1	-2.6± .4	.134±.008	27.7±1.9	1.00±.09
A	C8B4H2A1	-1.9± .6	.124±.012	26.3±3.0	.75±.14
A	C8H4B2A1	- .6± .7ns	.104±.013	23.0±3.3	.69±.16
A	H8B4C2A1	- .8± .5ns	.086±.010	18.7±2.4	.82±.12
A	H8C4B2A1	- .0± .6ns	.073±.013	16.7±3.1	.72±.15
B	A8C4H2B1	7.2± .6	.150±.012	40.8±3.0	.81±.14
B	A8H4C2B1	6.4± .6	.134±.012	36.4±2.9	.92±.14
B	C8A4H2B1	8.2± .6	.169±.012	46.0±2.9	.63±.14
B	C8H4A2B1	8.0± .5	.160±.011	44.0±2.7	.62±.13
B	H8A4C2B1	6.3± .6	.120±.012	33.4±2.9	.88±.14
B	H8C4A2B1	6.9± .6	.129±.011	35.8±2.8	.76±.13
C	A8B4H2C1	1.9± .5	.124±.009	30.3±2.2	.29±.11
C	A8H4B2C1	2.8± .5	.111±.011	28.4±2.6	.40±.13
C	B8A4H2C1	1.7± .3	.160±.007	38.2±1.7	.32±.08
C	B8H4A2C1	2.5± .3	.168±.007	40.8±1.6	.41±.08
C	H8B4A2C1	4.1± .5	.113±.010	30.6±2.4	.49±.12
C	H8A4B2C1	4.0± .4	.134±.008	35.1±1.9	.48±.09
H	A8B4C2H1	1.2± .5*	.097±.010	23.1±2.5	.96±.12
H	A8C4B2H1	2.8± .7	.101±.014	25.7±3.4	.94±.16
H	B8A4C2H1	- .7± .4ns	.132±.009	29.1±2.1	1.09±.10
H	B8C4A2H1	- .6± .5ns	.148±.011	33.0±2.6	1.14±.13
H	C8A4B2H1	3.6± .7	.134±.015	34.1±3.6	1.01±.17
H	C8B4A2H1	2.1± .7	.146±.013	35.4±3.2	1.07±.16
	A-B-C-H	2.5± .3	.129±.005	31.7±1.3	.76±.06

[a]Breed combinations (e.g., A-B) represent an average of the different mating types for that combination at equilibrium.
**P<.01. *P<.05. +P<.10. ns = nonsignificant (P>.10).

Similar results for Charolais and British breeds for WWT were reported by Alenda et al. (1980). Damon et al. (1961) found that the Hereford breed exceeded the Angus breed in general combining ability while Long and Gregory (1975) and Smith et al. (1976) reported different results for these British breeds. The large IgC and MgC effects and the small MgH effect for these traits partly explained the differences in preweaning performance of these breeds.

For the two-breed terminal crossing system, crossbred calves nursing either B or C dams generally had larger predicted ADG and WWT than those with A or H dams. A comparison of reciprocal crosses for the two-way mating system tended to suggest the importance of MgB and MgC effects for ADG and WWT. Charolais-sired calves that were reared by either A or H dams generally had low predicted ADG and WWT. This was partly because A and H dams were unable to provide sufficient milk and adequate mothering ability for the maximum growth of Charolais-sired crossbred calves (Dillard et al., 1980). Dillard et al. (1980) and Alenda et al. (1980) reported the maternal advantage of the C breed over that of H and A for the preweaning growth of their calves. Angus-Hereford and reciprocal crossed calves generally had the lowest predicted ADG and WWT. This was because of the large negative IgA and MgH effects on weaning traits.

For the 3-breed terminal system, Brahman-sired calves had the largest predicted ADG and WWT while Angus-sired calves had the smallest. Charolais- and Hereford-sired calves were intermediate in predicted ADG and WWT. Three-breed cross calves with more B or C breeding generally had larger predicted ADG and WWT than those with more A or H inheritance. This is a reflection of the significance of both the IgC and MgC effects and the MgB effect for the weaning traits. The small IgA, MgA, IgH and MgH effects and the large direct heterosis effects of Brahman crosses also partially accounted for these differences.

Least-squares constants for 2- and 3-breed backcrossing systems are shown in table 21. Charolais-sired 2-breed backcross calves had the greatest predicted ADG and WWT while those backcross calves sired by British bulls and reared by AH F1 cows had the smallest predicted WWT. Brahman-sired 2-breed backcross calves were intermediate in predicted ADG and WWT. For the 3-way backcross calves, those sired by C bulls had the largest predicted ADG and WWT while those sired by A or H bulls tended to have small predicted ADG and WWT.

Of primary importance were the IgC, MgC and MgB contributions to ADG and WWT compared to the small genetic effects associated with A and H breeds. Direct and maternal heterosis effects of crosses among these breeds apparently played a minor role in the ranking of their calves. However, Brahman crosses generally produced larger direct heterotic effects for these traits than most of the other crosses. Crockett et al. (1978) found significant heterosis advantages for preweaning ADG of Brahman x British crosses over British crosses. Alenda and Martin (1981) and Wyatt and Franke (1986) noted that the IgC effect was the major force shaping the responses of crosses associated with the C inheritance. Alenda and Martin (1981) also observed that direct and maternal heterosis effects were important in controlling the performance of crosses with varying proportions of A and H.

Least-squares constants for weaning traits of calves from the stabilized rotational systems are shown in table 22. Relative to the two-breed rotational crossbreeding system, the B-C breed combination had the largest predicted ADG and WWT while the A-H breed combination had the smallest. The A-B, A-C, B-H and C-H breed combinations were intermediate in predicted ADG and WWT. For the three-breed rotational crossing system in cyclic equilibrium, A-B-C and B-C-H breed combinations were predicted to gain faster and become heavier at weaning than A-B-H and A-C-H breed combinations. Brahman- and Charolais-sired four-breed rotational crosses in cyclic equilibrium generally had larger predicted ADG and WWT than Angus- and Hereford-sired calves. Breeds with large direct and maternal additive genetic effects such as C and crosses associated with large direct heterosis effects such as Brahman crosses contributed to differences in predicted ADG and WWT. The favorable maternal heterosis effects of Hereford crossbred dams also contributed to the large ADG and WWT of rotational crosses with H breeding.

General Discussion

Milk yields and preweaning performance in beef cattle have a high positive association (Rutledge et al., 1971; Reynolds et al., 1978; Franke and Martin, 1983; Daley et al., 1987). This relationship indicates that the volume of milk produced is a reflection of the maternal influence on weaning traits. Various studies have pointed to the superior milk production of Charolais dams over those of A or H (Melton et al., 1967; Franke and Martin, 1983), of A dams over those of H (Melton et al., 1967; Notter et al., 1978) and those of B over British dams (Hentges et al., 1963; Franke and Martin, 1983). Marshall et al. (1976) found no difference in milk yield between C and A cows.

Urick et al. (1986) suggested that the preweaning growth advantage of crossbred calves nursing AC and CH cows over those of AH cows was partly due to the greater level of milk production of Charolais-cross cows. Daley et al. (1987) found that, for 24-hour milk yield, AH cows had the highest milk production at 60 days while BH dams had the lowest. The AC and BA cows were intermediate in milk production at 60 days. However, at 150 days BA and AC cows had larger milk yields than BH and AH dams which were similar in milk production. They found daily yields of BA dams to increase as lactation progressed while the milk production levels of the other crossbred cows decreased or did not change.

Daley et al. (1987) found, from daily yields of all milk traits, Zebu crosses to be lower ($P<.01$) early in lactation than Bos taurus crosses except for protein percentage. Residual correlations between milk yield and preweaning ADG ranged from .36 to .45 at various stages of lactation. Component yields were highly correlated with preweaning ADG as well. Franke and Martin (1983), using rotational crossbred animals from this study, observed that milk yields of 3- and 4-breed crosses that included 1/8 Brahman breeding tended to decline linearly as lactation progressed. Those cows with 5/8 Brahman breeding tended to increase slightly in milk production from day 85 to day 152 and were essentially stable thereafter. Franke and Martin (1983) and Daley et al. (1987) found that Zebu cross mothers were more persistent milk producers than Bos taurus cross dams. This variation in milk production may be reflected in the differences in the predicted ADG and WWT for the progeny with these types of crossbred dams.

Condition Score. Least-squares constants for condition score are presented in tables 20, 21 and 22. Among the straightbreds, A had the highest SCORE while H had the lowest. The B and C breeds were intermediate in predicted

SCORE. Among the 2-breed crosses, only AB and its reciprocal and HA, HB and HC F1 crosses had significant predicted SCORE at weaning. Crossbred F1 calves raised by B cows and sired by British bulls had the largest predicted SCORE at weaning. Brahman cows were found to produce the most milk among the straightbred cows (Franke and Martin, 1983). These results imply that the high SCORE could be a reflection of the maternal ability of the dam. Hereford- and Brahman-sired three-breed cross calves nursing F1 cows tended to score more at weaning than Angus- and Charolais-sired calves nursing similar cows.

Relative to the two- and three-breed backcrossing systems, Angus- and Hereford-sired calves had the largest predicted SCORE, with Hereford-sired calves being greater in SCORE than Angus-sired calves. Two-and three-breed backcross calves with more A or H inheritance had greater SCORE than those with more B or C breeding. These results suggest the added importance of the MhAH effect over and above the large IgA and IgH effects on SCORE for backcross calves. Examination of 3-breed backcross calves also suggested that direct heterosis effects of B crosses and maternal heterosis effects of H crosses influenced SCORE of some of the crossbred progeny. Angus- and Hereford-sired calves raised by AH cows did not differ in SCORE. Results are in general agreement with those in the literature (Gregory et al., 1965; Pahnish et al., 1969; Long and Gregory, 1974; Gray et al., 1978). Backcross calves with high SCORE had a tendency to be associated with low WWT.

Relative to the stabilized rotational systems, Brahman x British and British x British breed combinations generally graded highest while Charolais crosses graded lowest at weaning. The two-breed rotational combinations were ranked on the basis of predicted SCORE in descending order as follows: B-H, A-B, A-H, C-H, A-C and B-C. For the three-breed rotational combinations in cyclic equilibrium, the A-B-H combination had the greatest predicted SCORE while the A-B-C combination had the lowest. The A-C-H and B-C-H rotational combinations were intermediate in predicted SCORE at weaning. Direct heterosis effects associated with Brahman x British crosses, the MhAH effect and the positive IgA and IgH effects accounted for most of the observed variation in SCORE for the rotational crossbreeding systems.

Charolais-sired crossbred calves have been reported to manifest excellent growth rate and generally poor gradability at weaning (Damon et al., 1959; Turner and McDonald, 1969). Damon et al. (1959) attributed this low SCORE to the lack of fatness in the Charolais crosses. Many studies have also supported the maternal advantage of A over H for SCORE (Sagebiel et al., 1974; Gray et al., 1978; Neville et al., 1984). A similar maternal effect of A and C for SCORE was reported by Dillard et al. (1980). Gaines et al. (1970) found nonsignificant differences among A and H for SCORE. Reports in the literature also tended to support the presence of considerable variability in the expression of heterosis for SCORE among various crosses (Rollins et al., 1969; Crockett et al., 1978; Drewry et al., 1978; Peacock et al., 1978, 1981).

Conclusion

Brahman-sired 2-breed terminal cross calves, Charolais-sired 2-breed terminal cross calves reared by B or H dams and Hereford-sired 2-breed terminal cross calves raised by C dams had the largest predicted BWT. Brahman-sired 3-breed terminal cross calves had the largest predicted BWT followed Hereford-sired calves raised by AC dams and Charolais-sired calves reared by AH or BH dams. Charolais-sired backcross calves had the largest predicted BWT followed by Hereford-sired backcross calves reared by CH or ACH dams.

Hereford-Brahman, HC, CB, BC, BA, AB and AC F1 crossbred calves had the largest predicted ADG, WWT and SCORE while AH, BH, CH and HA F1 crossbred calves had the lowest predicted ADG, WWT and SCORE. Most 3-breed terminal cross calves with B breeding and HAC calves had the largest predicted ADG and WWT while BAH and HCB calves had the largest predicted SCORE. Charolais-sired 2- and 3-breed backcross calves and B3C1 calves had the largest predicted ADG and WWT. Angus- and Hereford-sired backcross calves had the largest predicted SCORE.

All stabilized rotations with C inheritance had the largest predicted BWT. Most 2-breed stabilized rotational combinations with B breeding and the C-H rotational combination had the largest predicted ADG and WWT. Brahman-Angus and B-H rotational combinations had the largest predicted SCORE. Brahman- and Charolais-sired 2-breed stabilized rotations had the largest predicted ADG and WWT. Likewise, Hereford-sired BH and Angus-sired AB 2-breed stabilized rotations had the largest predicted SCORE. Most stabilized rotational crossbred calves with B and C breeding had the largest predicted ADG and WWT. Most Angus- and Hereford-sired stabilized rotational crosses had the largest predicted SCORE.

Beef cattle producers have a wide variety of breeds and mating systems to utilize for increased production. Evidently the choices of breed resources and mating systems constitute a mating plan and are closely linked. The producer has thus been provided with pertinent information for the joint selection of a mating system and breed combinations best adapted to meet his desired goals. However, other factors (e.g., reproduction cycles, postweaning performance, marketing environment, etc.) besides those considered in this study also impact on decisions relative to the efficiency of breeds and mating systems.

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CHAPTER IV

A COMPARISON OF REALIZED VS PREDICTED HETEROSIS ESTIMATES FOR PREWEANING TRAITS IN BEEF CATTLE

Summary

Data for this study came from four generations of a long-term rotational crossbreeding study at the Ben Hur Crossbreeding Research Unit of the Louisiana Agricultural Experiment Station. The nature of these data and the animals involved including the description of the management of the herds were provided in Chapter II. Two models were examined to determine the importance of effects other than dominance that may contribute to the expression of heterosis for birth weight (BWT), preweaning gain (ADG), weaning weight (WWT) and condition score (SCORE). Model I was used to fit constants for direct and maternal additive and heterosis genetic effects, effects due to sex-linkage and epistasis of all forms and any other unknown effects for each breed group. Model II was similar to model I except that the breed group effect was partitioned into direct (Ig) and maternal (Mg) additive and direct (Ih) and maternal (Mh) heterosis genetic effects. This separation into genetic effects was based on the assumptions of linearity between performance (heterosis) and heterozygosity (the dominance model) and of the complete determination of expected performance of the cross by the

linear combination of these genetic effects. An F-test was used to determine the adequacy of the additive-dominance model in describing the variability in preweaning traits of crosses produced in a rotational crossbreeding system. F-test results suggested that the regression model accounted for most of the variation for all preweaning traits. This was supported by the small differences between the R^2 values of the regression and breed group effects models. An attempt was made to compare estimates of realized heterosis with those of overall expected heterosis. Overall expected heterosis was computed assuming that the calf and dam components of heterosis combined additively and that hybrid vigor was linear with the theoretical genotypic heterozygosity with respect to breed of origin of the allelic pairs. Examination of differences between estimates of realized and overall expected heterosis suggested the presence of unaccountable variations which tested significant in most cases for BWT and ADG. Differences between these estimates for WWT and SCORE tended to be relatively unimportant.

(Key Words: Breed Group Effect, Regression Model, Heterozygosity, Dominance Model).

Introduction

Mendel in 1866 (Cunningham, 1987) laid the foundation of dominance effects in plant hybridization. Bruce (1910) used the dominance model to explain heterosis while Fisher (1918) provided the statistical model that included additive and dominance effects. This Fisher model was extended to include all forms of epistatic effects by Cockerham (1954). Gardner and Eberhart (1966) generalized the statistical-genetic model to encompass crossbreeding systems.

The dominance model (a major hypothesis for the explanation of heterosis) was elaborately described by Cunningham (1982, 1987) and Hill (1982) and experimentally validated by McGloughlin (1980), Koch et al. (1985), Morris et al. (1986) and Kress et al. (1986). Cunningham (1982) concluded from an evaluation of various studies involving mice, dogs, corn and beef cattle that the additive-dominance model was adequate. Sheridan (1981), however, demonstrated the insufficiency of the dominance model from an analysis of poultry data.

The underlying assumption for the dominance model is the linear dependence of performance (heterosis) on the degree of heterozygosity in the crossbred individual. Dickerson (1969, 1973) coined the term "recombination loss" to describe any deviation from this linear association. Different attempts have been made to model epistatic recombination effects for different types of crosses assuming a two-locus epistasis model (Dickerson, 1969, 1973; Kinghorn, 1980; Hill, 1982; Koch et al., 1985). Koch et al. (1985) reported the likely loss of beneficial epistatic effects in backcross generations and in rotational populations. This was suggestive of an expected decrease in performance when predicted solely on the basis of the additive-dominance model.

Rastogi et al. (1982), working with data from sheep breeding, concluded that recombination effects were small but favorable, with mean values ranging from 1.4 % for BWT to 5.7 % for ADG. However, empirical evidence tends to suggest that epistatic recombination losses are not important in beef and sheep breeding (Tewolde, 1981; Koch et al., 1985; Morris et al ., 1986). Others have provided similar conclusions based on a comparative study of R^2 values from both breed group effects and genetic effects models (Koger et al., 1975; Dillard et al., 1980; Robison et al., 1981; Quintana and Robison, 1983; Neville et al., 1984).

Dickerson (1969) derived genetic expectations for recombination losses in the maternal and progeny performance to be: 1/3 for the 2-breed, 3/7 for the 3-breed and 7/15 for the 4-breed rotations. McDonald (1972) suggested, however, that recombination effects may be relatively unimportant in rotational systems utilizing straightbred sires. This is because only the crossbred females are likely to produce recombination gametes.

The objectives of this study were:

1) to determine the adequacy of the dominance model, and
2) to compare two approaches for estimating heterosis.

Materials and Methods

The description of the data used in this study was provided in Chapter II. These data came from 4 straightbred lines (A, B, C, H) and 7 crossbred lines (A-B, C-B and H-B two-breed, A-B-C, C-B-H and H-B-C three-breed and A-B-C-H four-breed rotational combinations) involved in a long-term rotational crossbreeding program at the Ben Hur Crossbreeding Research Unit of the Louisiana Agricultural Experiment Station. Among the preweaning traits examined were birth weight (BWT), preweaning daily gain (ADG), weaning weight (WWT) and condition score (SCORE).

Statistical Procedures

Statistical Models. The breed group effects model (model I) was designed to take account of all the genetic effects including direct and maternal additive and heterosis genetic effects, effects due to sex-linkage and all forms of epistasis and any unknown factors. In addition, this model contained the overall mean and the nongenetic effects of sex, generation-year subclass, weaning age of calf in days, Julian birthdate of calf in days, cow age in years and a random error term. The genetic model (model II) consisted of the overall mean and the nongenetic effects as for model I and a partition of the breed group effects into the direct and maternal additive (Igi and Mgi) and direct and maternal heterosis (Ihij and Mhij) genetic effects and a random error term.

The genetic model was based on the following assumptions:

1) That the breed group effects were completely determined by the linear association of the additive direct (Ig) and maternal (Mg) effects (for the straightbreds) plus the heterosis direct (Ih) and (or) maternal (Mh) effects (for the crossbreds).

2) That independent loci affected each of the preweaning traits.

Consequently, any differences between breed group effects and genetic effects models should reflect nonlinear genetic effects, effects due to all forms of epistasis and to sex-linkage and any unknown factors (Dickerson, 1969, 1973; Robison et al., 1981; Quintana and Robison, 1983). Comparison of such statistics as the R^2 values from these two models should provide relative information as to the adequacy or inadequacy of the additive-dominance model. An F-test, based on the "Extra Sum of Squares" principle (Draper and Smith, 1981) was used to test the significance in the reduction in sums of squares due to the addition of other genetic effects to the reduced model (R). This test was developed as follows:

$$F \text{ ratio} = [SSE(R) - SSE(F)]/[df_R - df_F] + SSE(F)/df_F,$$

where, R denotes the regression model,

F denotes the breed group model,

SSE denotes sums of squares due to error, and

df denotes degrees of freedom.

To determine the validity of the models used in this study, two kinds of models were compared:

a) Breed group model (model I):

$$Y = mu + gy + sex + b1\ (A - 227.5) + b2\ (D - 5.5) + c1\ (A - 227.5)^2 + c2\ (D - 5.5)^2 + line/generation + error,$$

b) Genetic or regression model (model II):

$$Y = mu + gy + sex + b1\ (A - 227.5) + b2\ (D - 5.5) + c1\ (A - 227.5)^2 + c2\ (D - 5.5)^2 + Z_{pq} + error,$$

where,

Y = response variable measured on each calf (BWT, ADG, WWT, SCORE),

mu = overall mean,

gy = generation-year subclass effect,

b1 and b2 = partial linear regression on calf age at weaning (or Julian birthdate in the case of BWT) in days and dam age at calf birth in years, respectively, c1 and c2 = partial quadratic regression on calf weaning age (or Julian birthdate in the case of BWT) and age of dam at calf birth, respectively,

line/generation = breed group effects,

Z_{pq} = genetic effects (see model in Chapter II).

Heterosis Estimation. Expected heterosis (Y) was computed using estimates of the calf and dam heterotic genetic effects and their corresponding measures of breed heterozygosity as shown in tables 10a and 10b. Modelling of the expected heterosis was based on the following premises:

1) that a linear relationship exists between heterosis and degree of breed heterozygosity,

2) that the overall expected heterosis is a linear function of the calf and dam components of heterosis, and

3) that heterosis depends only on dominance effects (i.e., that epistatic and recombination loss effects are assumed to be unimportant).

Overall Expected Heterosis in calf (Y) = (percentage heterozygosity in calf) (calf heterotic genetic effect) + (percentage heterozygosity in dam of calf) (dam heterotic genetic effect).

Robison et al. (1981) and Neville et al. (1984) suggested that the regression model provided accurate and efficient estimates of the genetic effects. It also allows for the separation of heterosis effects into the calf and dam components, thus enabling the estimation of expected heterosis in the calf and the dam separately.

Realized heterosis is a composite estimate of nonadditive genetic effects. It consists of the calf and dam components of heterosis (hybrid vigor) plus any interactions that may be present. Realized heterosis (X) was calculated using the traditional method of comparing the average performance of crossbred offspring with the weighted performance of their straightbred parental breeds. Estimates of realized heterosis for the calf traits were calculated taking into account the breed composition of the calf as follows:

1) Two-breed backcross heterosis = [HxHB] - [3/4(H) + 1/4(B)];

2) Three-breed heterosis = [CxHB] - [1/2(C) + 1/4(H) + 1/4(B)];

and

3) Four-breed heterosis = [CxHAB] - [1/2(C) + 1/4(H) + 1/8(A) + 1/8(B)].

Differences between realized and estimated heterosis for each preweaning trait should, therefore, reflect the accuracy or error associated with predicting heterosis using the genetic model approach. Sellier (1976) suggested that the discrepancies between heterosis as measured and heterosis as expected from a genetic model including only additive and dominance effects can arise from the recombination between genes from parental breeds when crossing crossbred parents. The result of this recombination between genes is the modification of epistatic deviations in the offspring.

Statistical Analysis. Realized heterosis was estimated using linear contrast procedures in SAS (1982) and the breed group model. Expected heterosis was estimated using linear contrast procedures in SAS (1982) and the regression model. Expected heterosis was estimated separately for the calf and dam components and summed to obtain overall expected heterosis for each cross. The difference between realized and overall expected heterosis estimates for each cross were tested for significance using a conservative t-test. The conservative "t" value for this test was obtained by dividing this difference by the larger of the standard errors for the respective estimates.

Results and Discussion

Comparison of Models I and II

Table 23 presents a comparison between the regression (model II) and the breed group effects (model I) models. Model I fitted constants for each genetic group that included direct and maternal additive and heterotic genetic effects, nonlinear effects, effects associated with epistatic recombination loss and sex-linkage, grandmaternal additive and heterotic effects and any unknown factors.

TABLE 23. COMPARISON OF BREED GROUP VS GENETIC MODEL FOR PREWEANING TRAITS

Trait[a]	Model[b]	df	Error sums of squares	Error mean squares	F ratio[c]	%[d]	R^2 %
BWT	Genetic	2908	61605.66				44.6
	Breed	2886	59559.51				46.5
	Reduction	22	2046.15	93.01	4.51**	3.4	
	Error	2886	59559.51	20.64			
ADG	Genetic	2908	24.65				54.7
	Breed	2886	23.90				56.1
	Reduction	22	.75	.0341	4.11**	3.1	
	Error	2886	23.90	.0083			
WWT	Genetic	2908	1498167.00				62.1
	Breed	2886	1455791.53				63.1
	Reduction	22	42375.47	1926.16	3.82**	2.9	
	Error	2886	1455791.53	504.43			
SCORE	Genetic	2908	3455.08				44.1
	Breed	2886	3395.64				45.1
	Reduction	22	59.44	2.70	2.29**	1.8	
	Error	2886	3395.64	1.18			

[a]Preweaning traits where BWT = Birth weight, ADG = preweaning gain, WWT = weaning weight and SCORE = condition score.
[b]Genetic model (R) - breed group model (F) = reduction.
[c]F ratio test for significance due to reductions in sums of squares for the two models.
[d]Percentage reduction in sums of squares for the two models was calculated as follows:
(Reduction sums of squares error)/(Breed group sums of squares error) * 100.
**P<.01.

Model II was a simplified version of Model I which took account only of direct and maternal additive and heterotic genetic effects. Thus, differences in the residual mean squares of these two models should reflect nonlinear genetic effects, effects due to sex-linkage and all forms of epistasis and any unknown factors (Robison et al., 1981; Quintana and Robison, 1983; Neville et al., 1984). The grandmaternal additive and heterotic genetic effects were assumed to be neligible.

Nonlinear genetic effects refer to all possible interactions among the additive and dominance effects (Dickerson, 1969; Hill, 1982). Malik (1984) defined epistatic recombination loss as that effect which occurs in advanced generations (rotations, backcrosses, synthetics etc.) of crossbreeding as a result of segregation and recombination of genes brought together from two purebred parents in an F1 generation.

Percentage reductions for all traits examined ranged from 1.8 to 3.4; which were higher than those reported by Dillard et al. (1980) and Neville et al. (1984) for these same traits. The additional reduction due to such factors as epistasis, sex-linkage and any unknown factors was significant for all preweaning traits. However, the magnitude of the F values was relatively small. This was generally in agreement with the results of other workers (Dillard et al., 1980; Robison et al., 1981; Neville et al., 1984). Quintana and Robison (1983), using swine data, found that this extra reduction was nonsignificant. In addition, the R^2 values for the two models were similar for all traits, suggesting that the same amount of variation was explained by the regression and breed group effects models.

Therefore, variation in the preweaning traits was satisfactorily accounted for by including only direct and maternal additive and heterotic genetic effects in the regression model. Consequently, estimates of the genetic parameters obtained in this current study should be appropriate for the prediction of additional crosses (Quintana and Robison, 1983).

Comparison of Realized vs Expected Heterosis

Estimates of realized heterosis, expected heterosis in the calf and dam, respectively, overall expected heterosis in calf and differences between realized and overall expected heterosis estimates for BWT, ADG, WWT, and SCORE are presented in tables 24, 25, 26 and 27, respectively. Realized heterosis values for all traits were generally in agreement with those reported by Tucker (1985) for generations 1, 2 and 3 of this same study.

The calf component of expected heterosis was the principle determinant of the magnitude of the estimates of overall expected heterosis for all preweaning traits. The dam component of expected heterosis, generally expressed as a permanent environmental effect on calf performance, tended to negate overall expected heterosis estimates for most preweaning traits. Generally the maternal component of expected heterosis was less than that of the calf.

Differences between estimates of realized and overall expected heterosis were mostly significant for BWT and ADG. These results seem to agree with those of Rastogi et al. (1982) relative to sheep. No consistent pattern was found among these differences for each generation of rotational crossbreeding. Alenda and Martin (1981) noted that sex-linkage and environmental effects generally tended to produce cyclical patterns of performance over generations. Although the expected level of retention of heterosis in rotational crossbreeding systems has been shown to be maintained (Tucker, 1985; Urick et al., 1986), Alenda and Martin (1981) contended that this level was modifiable if epistatic effects were large.

Because realized heterosis takes into consideration the calf and dam components of heterosis plus any unexplained heterosis, any significant difference between its estimate and that of overall expected heterosis should reflect this unexplained variation. This unexplained heterosis could partly represent the modified epistatic contributions (Sellier, 1976; Alenda and Martin, 1981) and partly represent errors due to methods of estimation. Thus suggesting that recombination loss effects can be either positive or negative, contrary to Dickerson's hypothesis (1969). However, Tewolde (1981), Koch et al. (1985) and Morris et al. (1986) found no favorable effects of recombination loss for preweaning traits in sheep and beef cattle.

<u>Conclusion</u>

The regression model is the model of choice. It is a simple and easily interpretable model. The regression model allows for the derivation of accurate and efficient estimates of the calf component of heterosis and the dam component of heterosis. The comparison of realized with expected heterosis suggested the presence of unaccounted variation in the expression of heterosis (hybrid vigor). Most of the differences between realized and expected heterosis were significant for BWT and ADG. The magnitude and direction of these differences suggested either the presence of recombination loss effects or sampling variation in the estimates of heterosis or both.

TABLE 24. REALIZED VS EXPECTED HETEROSIS FOR BIRTH WEIGHT BY LINE AND GENERATION (kg)

Line	Realized heterosis[a] (X)	Expected heterosis[b] in: Calf	Dam	Calf+Dam (Y)	Difference (X-Y)[c]
		GENERATION 1			
A3B1	-1.0± .6+	2.9± .7**	-2.3±1.1*	.7± .6	-1.7**
C3B1	-1.9± .6**	3.2± .6**	-3.9±1.1**	-.7± .6	-1.2*
H3B1	- .2± .6	2.9± .6**	-2.0±1.2+	.9± .6	-1.1+
C2B1A1	-1.6± .6**	2.3±1.0*	-2.3±1.1*	.0± .7	-1.6**
A2B1H1	- .0± .5	4.2± .9**	-2.0±1.2+	2.2± .7**	-2.2**
C2B1H1	1.3± .6*	4.6±1.0**	-2.0±1.2+	2.6± .7**	-1.3+
H2B1A1	1.6± .6**	4.2± .9**	-2.3±1.1*	1.9± .7**	- .3
		GENERATION 2			
B5A3	5.6± .7**	4.4±1.0**	-1.1± .6*	3.3± .5**	2.3**
B5C3	4.3± .7**	4.9±1.0**	-2.0± .6**	2.9± .5**	1.4*
B5H3	5.0± .7**	4.3±1.0**	-1.0± .6+	3.3± .5**	1.7*
A5C2B1	-1.5± .6**	.5± .8	-1.3± .9	-.8± .6	- .7
H5A2B1	1.2± .6+	2.7± .6**	- .7± .8	2.0± .5**	- .8
H5C2B1	- .2± .6	2.8± .8**	-1.7± .9*	1.1± .5*	-1.3*
C4H2B1A1	1.7± .6**	2.5± .9**	- .6± .9	1.9± .6**	- .2
		GENERATION 3			
A11B5	- .3± .7	3.7± .8**	-1.7± .9*	2.0± .4**	-2.3**
C11B5	1.1± .6+	4.1± .8**	-2.9± .8**	1.1± .4**	.0
H11B5	.2± .6	3.6± .8**	-1.5± .9+	2.1± .3**	-1.9**
B9A5C2	7.6± .6**	5.3±1.1**	.1± .7	5.4± .8**	2.2**
B9H5A2	7.2± .6**	5.1±1.1**	- .1± .6	5.0± .8**	2.2**
B9H5C2	7.1± .6**	5.2±1.1**	- .3± .7	5.0± .8**	2.1**
B9C4H2A1	8.8± .6**	5.4±1.1**	- .4± .8	5.0± .8**	3.8**
		GENERATION 4			
B21A11	5.3±1.2**	4.0± .9**	-1.4± .7*	2.6± .4**	2.7*
B21C11	2.5±1.2*	4.5± .9**	-2.5± .7**	2.0± .4**	.5
B21H11	4.9±1.2**	4.0± .9**	-1.3± .7+	2.7± .4**	2.2+
C18B9A5	-2.6±1.2*	3.1± .9**	-2.4±1.0**	.7± .5	-3.3**
A18B9H5	.1±1.1	4.1± .9**	-1.8±1.0+	2.3± .4**	-2.2*
C18B9H5	-4.8±1.2**	4.5± .9**	-2.2±1.0*	2.3± .5**	-7.1**
A17B9C4H2	- .3±1.1	3.1± .9**	-2.7±1.0**	.4± .6	- .7

[a]Estimate was obtained using the breed group model (I) and the computational definition of heterosis (crossbred average minus weighted straightbred performance).
[b]Estimate was derived from the genetic model (II) and using breed heterozygosity.
[c]This is the difference between the realized and expected heterosis which was tested using a conservative t-test.
**P<.01. *P<.05. +P<.10.

TABLE 25. REALIZED VS EXPECTED HETEROSIS FOR ADG BY LINE AND GENERATION (kg/d)

Line	Realized heterosis[a] (X)	Expected heterosis[b] in: Calf	Dam	Calf+Dam (Y)	Difference (X-Y)[c]
		GENERATION 1			
A3B1	.13±.01**	.08±.01**	.01±.02	.09±.01**	.04**
C3B1	.06±.01**	.06±.01**	.00±.02	.07±.01**	-.01
H3B1	.17±.01**	.07±.01**	.07±.02**	.14±.01**	.03*
C2B1A1	.09±.01**	.09±.02**	.01±.02	.10±.01**	-.01
A2B1H1	.18±.01**	.10±.01**	.07±.02**	.17±.01**	.01
C2B1H1	.15±.01**	.10±.02**	.07±.02**	.17±.01**	-.02
H2B1A1	.17±.01**	.09±.02**	.01±.02	.10±.01**	.07**
		GENERATION 2			
B5A3	.10±.01**	.12±.02**	.01±.01	.13±.01**	-.03*
B5C3	.09±.01**	.10±.02**	.00±.01	.10±.01**	-.01
B5H3	.07±.01**	.10±.02**	.04±.01**	.14±.01**	-.07**
A5C2B1	.11±.01**	.07±.02**	.02±.02	.09±.01**	.02
H5A2B1	.16±.01**	.06±.01**	.04±.02*	.10±.01**	.06**
H5C2B1	.15±.01**	.07±.02**	.03±.02+	.10±.01**	.05**
C4H2B1A1	.07±.01**	.08±.02**	.07±.02**	.15±.01**	-.08**
		GENERATION 3			
A11B5	.13±.01**	.10±.02**	.01±.02	.11±.01**	.02
C11B5	.10±.01**	.08±.02**	.00±.02	.08±.01**	.02
H11B5	.19±.01**	.08±.02**	.05±.02**	.14±.01**	.05**
B9A5C2	.11±.01**	.13±.02**	.02±.02	.15±.02**	-.04**
B9H5A2	.11±.01**	.12±.02**	.05±.01**	.18±.02**	-.07**
B9H5C2	.11±.01**	.12±.02**	.05±.01**	.16±.02**	-.05**
B9C4H2A1	.13±.01**	.12±.02**	.04±.02**	.16±.02**	-.03
		GENERATION 4			
B21A11	.09±.02**	.11±.02**	.01±.01	.12±.01**	-.03
B21C11	.07±.02**	.09±.02**	.00±.01	.09±.01**	-.02
B21H11	.06±.03**	.09±.02**	.04±.02**	.14±.01**	-.08**
C18B9A5	.08±.02**	.09±.02**	.01±.02	.10±.01**	-.02
A18B9H5	.13±.02**	.10±.02**	.05±.02*	.15±.01**	-.02
C18B9H5	.10±.02**	.09±.02**	.05±.02*	.14±.01**	-.04
A17B9C4H2	.16±.02**	.11±.02**	.02±.02	.13±.01**	.03

[a]Estimate was obtained using the breed group model (I) and the computational definition of heterosis (crossbred average minus weighted straightbred performance).
[b]Estimate was derived from the genetic model (II) and using breed heterozygosity.
[c]This is the difference between the realized and expected heterosis which was tested using a conservative t-test.
**P<.01. *P<.05. +P<.10.

TABLE 26. REALIZED VS EXPECTED HETEROSIS FOR WEANING WEIGHT BY LINE AND GENERATION (kg)

		Expected heterosis[b] in			
Line	Realized heterosis[a] (X)	Calf	Dam	Calf+Dam (Y)	Difference (X-Y)[c]
		GENERATION 1			
	**	**			
A3B1	27.5±3.1	20.9±3.2	.6±5.6	21.5±3.0**	6.0+
C3B1	11.2±3.1	17.2±3.2	-3.6±5.5	13.5±3.0**	-2.3
H3B1	36.7±3.2	17.7±3.2	13.9±5.7*	31.7±3.0**	5.0
C2B1A1	18.0±3.0	22.2±4.9	.6±5.6	22.9±3.3**	-4.9
A2B1H1	40.3±2.6	27.4±4.4	13.9±5.7*	41.3±3.2**	-1.0
C2B1H1	35.4±3.0	26.3±4.8	13.9±5.7*	40.2±3.2**	-4.8
H2B1A1	39.2±3.0	24.2±4.5	.6±5.6	24.8±3.3**	14.4**
		GENERATION 2			
	**	**			
B5A3	27.1±3.4	31.4±4.8	.3±2.8	31.7±2.5**	-4.6
B5C3	22.8±3.4	25.7±4.8	1.8±2.7	23.9±2.6**	-1.1
B5H3	20.5±3.3	26.6±4.8	7.0±2.9*	33.5±2.4**	13.0**
A5C2B1	23.6±3.0	15.5±3.9	3.2±4.4	18.7±2.7**	4.9
H5A2B1	37.9±3.0	15.3±3.2	8.6±4.2*	23.9±2.4**	14.0**
H5C2B1	35.3±3.0	18.0±3.8	4.9±4.2	22.9±2.6**	12.4**
C4H2B1A1	19.0±3.1	20.3±4.3	15.3±4.2**	35.5±3.1**	-16.5**
		GENERATION 3			
	**	**			
A11B5	30.4±3.2	26.1±4.0	.5±4.2	26.6±1.7**	3.8
C11B5	23.1±3.2	21.4±4.0	-2.7±4.1	18.7±1.8**	4.4
H11B5	43.4±2.9	22.1±4.0	10.5±4.3*	32.6±1.7**	10.8**
B9A5C2	31.1±3.1	34.7±5.4	5.1±3.7	39.8±4.0**	-8.7*
B9H5A2	31.8±3.1	32.6±5.4	11.8±3.1**	44.4±3.9**	-12.6**
B9H5C2	31.8±3.1	30.7±5.4	10.2±3.4**	41.0±3.7**	-9.2*
B9C4H2A1	37.9±3.1	31.2±5.3	8.3±3.9*	39.6±3.8**	-1.7
		GENERATION 4			
	**	**			
B21A11	26.8±6.0	28.7±4.4	.4±3.5	29.1±1.9**	-2.3
B21C11	18.2±5.9	23.6±4.4	-2.3±3.4	21.3±1.9**	-3.1
B21H11	20.3±6.1	24.4±4.4	8.7±3.6*	33.1±1.8**	-12.8*
C18B9A5	15.4±5.8	22.5±4.4	- .5±4.7	22.0±2.3**	-6.6
A18B9H5	30.1±5.4	27.6±4.2	8.9±4.9+	36.4±2.2**	-6.3
C18B9H5	19.5±5.7	25.0±4.4	7.8±4.8+	32.8±2.2**	-13.3*
A17B9C4H2	35.8±5.5	27.7±4.6	1.8±4.7	29.4±2.9**	6.4

[a]Estimate was obtained using the breed group model (I) and the computational definition of heterosis (crossbred average minus weighted straightbred performance).
[b]Estimate was derived from the genetic model (II) and using breed heterozygosity.
[c]This difference was tested using a conservative t-test
**P<.01. *P<.05. +P<.10.

TABLE 27. REALIZED VS EXPECTED HETEROSIS FOR CONDITION SCORE BY LINE AND GENERATION (units)

Line	Realized heterosis[a] (X)	Expected heterosis[b] in: Calf	Dam	Calf+Dam (Y)	Difference (X-Y)[c]
		GENERATION 1			
A3B1	.63±.15**	.49±.15**	-.09±.27	.40±.15**	.23
C3B1	.08±.15	.26±.15+	-.05±.26	.21±.14	-.13
H3B1	1.00±.15**	.43±.15**	.47±.27+	.90±.15**	.10
C2B1A1	.10±.15	.32±.23	-.09±.27	.23±.16	-.13
A2B1H1	1.02±.13**	.55±.21**	.47±.27+	1.02±.16**	.00
C2B1H1	.58±.14**	.49±.23*	.47±.27+	.96±.16**	-.38*
H2B1A1	.85±.14**	.50±.21*	-.09±.27	.41±.16**	.44**
		GENERATION 2			
B5A3	.71±.16**	.74±.23**	-.04±.14	.69±.12**	.02
B5C3	.46±.17**	.39±.23+	-.03±.13	.37±.12**	.09
B5H3	.58±.16**	.65±.23**	.23±.14+	.88±.12**	-.30+
A5C2B1	.59±.15**	.31±.19+	.04±.21	.35±.13**	.24
H5A2B1	1.19±.15**	.28±.15+	.34±.20+	.62±.12**	.57**
H5C2B1	1.24±.15**	.44±.18*	.26±.20	.70±.13**	.54**
C4H2B1A1	.62±.15**	.39±.21+	.62±.20**	1.01±.15**	-.39**
		GENERATION 3			
A11B5	.75±.16**	.61±.19**	-.07±.20	.55±.08**	.20
C11B5	.53±.15**	.33±.19+	-.04±.20	.29±.09**	.24
H11B5	1.49±.14**	.54±.19**	.35±.21+	.89±.08**	.60**
B9A5C2	.40±.15**	.74±.26**	.05±.18	.79±.19**	-.39*
B9H5A2	.65±.15**	.79±.26**	.50±.15**	1.29±.19**	-.64**
B9H5C2	.63±.15**	.67±.26**	.40±.16**	1.07±.18**	-.44*
B9C4H2A1	.66±.15**	.60±.25*	.30±.19+	.90±.18**	-.24
		GENERATION 4			
B21A11	.60±.29*	.67±.21**	-.06±.17	.62±.09**	-.02
B21C11	.24±.29	.36±.21+	-.03±.17	.33±.09**	-.09
B21H11	.41±.30	.59±.21**	.29±.17+	.89±.08**	-.48
C18B9A5	.13±.28	.33±.21+	-.07±.23	.26±.11*	-.13
A18B9H5	.33±.26	.59±.20**	.27±.23	.86±.10**	-.53*
C18B9H5	.39±.28	.44±.21*	.28±.23	.72±.11**	-.33
A17B9C4H2	.54±.27*	.60±.22**	.08±.22	.68±.14**	-.14

[a]Estimate was obtained using the breed group model (I) and the computational definition of heterosis (crossbred average minus weighted straightbred performance).
[b]Estimate was derived from the genetic model (II) and using breed heterozygosity.
[c]This difference was tested using a conservative t-test
**P<.01. *P<.05. +P<.10.

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CHAPTER V

CONCLUSIONS

The following conclusions can be made from this entire study:

1) The Charolais had the largest Ig estimate for BWT, ADG and WWT while H had the largest Ig estimate for SCORE.

2) Angus and Charolais had similar and larger Mg estimates for BWT than H and B while A and B had the lowest Ig and Mg estimates, respectively, for BWT.

3) Brahman and Charolais had similar and larger Mg estimates for ADG, WWT and SCORE than A and H while H had the lowest Mg estimate for all preweaning traits except BWT.

4) Brahman crosses (AB, BC and BH) had the largest Ih estimates for all preweaning traits. Brahman crosses also had the lowest Mh estimates for BWT. With the exception of BH, Brahman crosses had the lowest Mh estimates for ADG, WWT and SCORE.

5) Hereford crosses (AH, BH and CH) had the largest Mh estimates for ADG, WWT and SCORE.

6) As deviations from Hereford, the respective A, B and C Ig estimates were -2.8 ± .8 ($P<.01$), 1.8 ± 1.2 and 6.6 ± .9 ($P<.01$) kg for BWT; -.04 ± .02 ($P<.01$), -.06 ± .03 ($P<.05$) and .07 ± .02 ($P<.01$) kg/d for ADG; -12.0 ± 4.1 ($P<.01$), -9.3 ± 6.1 and 22.4 ± 4.6 ($P<.01$) kg for WWT and -.35 ± .20, -1.34 ± .29 ($P<.01$) and -1.21 ± .22 ($P<.01$) for SCORE.

7) When deviated from Hereford, the respective A, B and C Mg estimates were 1.0 ± .8, -5.0 ± 1.2 ($P<.01$) and .8 ± .9 kg for BWT; .09 ± .02 ($P<.01$), .18 ± .02 ($P<.01$) and .16 ± .02 ($P<.01$) kg/d for ADG; 21.2 ± 4.1 ($P<.01$), 34.7 ± 5.9 ($P<.01$) and 36.0 ± 4.6 ($P<.01$) kg for WWT and .93 ± .20 ($P<.01$), 1.52 ± .28 ($P<.01$) and 1.34 ± .22 ($P<.01$) for SCORE.

8) Brahman- and Charolais-sired crossbred calves generally had the largest predicted BWT, ADG and WWT.

9) Straightbred Charolais calves and BC and CB two-breed terminal crossbred calves had the largest predicted BWT, ADG and WWT while AB and HB two-breed terminal crossbred calves had the largest predicted SCORE.

10) For the two- and three-breed stabilized rotations, all crossbred calves with more Brahman and Charolais inheritance generally had the largest predicted BWT, ADG and WWT while those with more Angus and Hereford inheritance had the largest predicted SCORE.

11) The Ig, Mg and Ih genetic effects were found to contribute substantially to variation in BWT while Ig and Mg genetic effects were important sources of variation for SCORE. All genetic effects (Ig, Mg, Ih and Mh) were important sources of variation for ADG and WWT.

12) Comparisons of breed group vs genetic models suggested that epistatic and linkage effects did not contribute significantly to differences among breeding groups.

13) Comparisons of differences among realized and expected heterosis suggested the presence of recombination loss effects among rotational crosses. The sign of these differences also suggested that recombination loss effects may be positive or negative.

Vita

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Major Field: Animal Science

Title of Dissertation: Estimation of Direct and Maternal Additive and Heterotic Genetic Effects for Preweaning Traits in Beef Cattle

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